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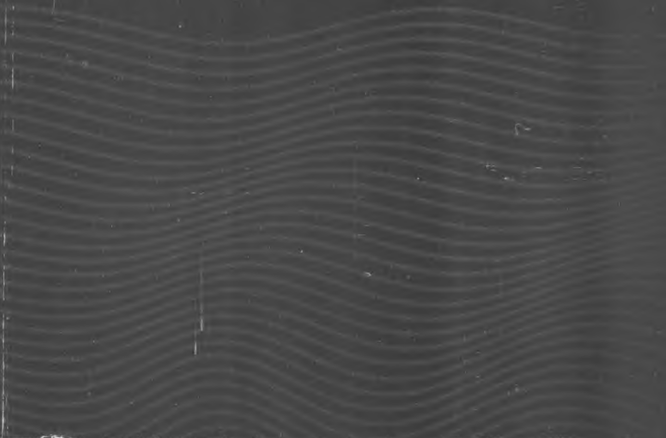

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The Quantification of Stream Drift

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Allan, J. D., and E. Russek. 1985. The quantification of stream drift. Can. J. Fish. Aquat. Sci. 42: 210–215.

Although the purpose of many drift studies is to describe quantitatively the abundance of drifting invertebrates and make comparisons between seasons or sites, almost no investigations have employed replicate sampling. We analyzed drift collections from a Rocky Mountain stream in order to investigate the variability of drift sampling. The data were normalized and the variances stabilized for each taxon examined by data transformation. The fourth root transformation was favored for five taxa and the logarithmic transformation for three. Using the 95% confidence limits on 24-h drift density for an abundant mayfly (*Baetis bicaudatus*), we found that six to seven replicates are required to obtain 95% CL ± 50% of the mean. Drift sampling appears to require fewer replicates than benthic sampling for comparable precision. Investigators may fail to replicate drift samples because they elect to sample frequently over 24 h in order to quantify the diel periodicity of drift. However, when comparison between sites or dates is the principal goal, we recommend that the effort normally put into frequent sampling over 24 h be invested instead in replicated sampling just after dark, when drift normally is greatest. When we regressed drift from the first night sample against total drift from the remainder of the 24-h period, 60–90% of the variation in the latter was predicted from the single nighttime sample. Thus, little information appears to be lost by this recommended procedure.

Bien qu'un grand nombre d'études sur les organismes dérivants consistent à décrire quantitativement l'abondance des invertébrés qui en dérivent et à faire des comparaisons entre les saisons et les emplacements, presqu'aucun chercheur ne s'est servi de la technique d'échantillonnage répété. Nous avons analysé des organismes dérivants prélevés dans un cours d'eau des Rocheuses afin d'étudier la variabilité de l'échantillonnage de ces organismes. Nous avons normalisé les données et stabilisé les variances obtenues pour chaque taxon examiné en transformant les données. La transformation par la racine quatrième a été choisie pour cinq taxons et la transformation logarithmique pour trois. En utilisant une limite de confiance de 95 % sur une densité d'organismes dérivants calculée pendant 24 h pour une espèce d'éphémère abondante (*Baetis bicaudatus*), nous avons trouvé que de six à sept échantillons répétés étaient nécessaires pour obtenir une LC de 95 % ± 50 % de la moyenne. L'échantillonnage d'organismes dérivants semble exiger moins d'échantillons répétés que l'échantillonnage d'organismes benthiques pour une précision comparable. Il se peut que les chercheurs omettent de répéter les échantillons d'organismes dérivants parce qu'ils préfèrent échantillonner fréquemment sur une période de 24 h afin de quantifier la périodicité nycthémérale des organismes dérivants. Cependant, lorsque la comparaison entre les emplacements ou les dates est le principal objectif visé, nous recommandons que l'effort fourni normalement pour prélever fréquemment des échantillons sur une période de 24 h soit plutôt consacré à prélever des échantillons répétés juste après la tombée de la nuit, lorsque le nombre d'organismes dérivants est normalement à son maximum. Quand nous avons calculé la régression des organismes dérivants pour le reste de la période de 24 h, nous avons prédit 60 à 90 % de la variation de ces derniers à partir de l'unique échantillon de nuit. Par conséquent, il semble que peu d'informations soient perdues lorsqu'on utilise la procédure recommandée.

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Drift, the downstream transport of organisms in running waters, has been of interest to stream biologists since Müller (1954) first reported this phenomenon. Diel periodicity, the potential consequences for invertebrate distribution, possible causes of drift activity, and its quantitative reporting have resulted in many studies (see reviews by Waters 1972; Müller 1974). Drift also provides a measure of invertebrate abundance that may be used to answer questions concerning comparisons from experimental manipulations or environmental impacts. In contrast with the sampling of stream benthos, however, where the issues of appropriate statistical methods, precision, and confidence limits have received extensive discussion (Elliott 1977; Green 1979; Resh 1979), the quantification of drift has received little study. Only Chutter (1975) specifically investigated variability of replicate drift collections, although Elliott's (1970) treatment of sampling methodology includes statistical examples using replicated nets, and Ulfstrand (1968) compared drift collections from several depths and locations within a site. Virtually without exception, however, reports of drift lack statements of the precision of estimate.

Topics that have been addressed for benthic sampling include the need for suitable data transformation (Downing 1979) so that assumptions of parametric statistics are satisfied, how sample size affects confidence limits around the mean (Resh 1979), and recommendations as to the suitability of various statistical procedures (Elliott 1977; Green 1979). Drift methodology has been discussed from the standpoints of collecting apparatus, various ways of calculating drift, and some aspects of statistical analysis (Elliott 1970; Waters 1969). However, data transformation and confidence limits around the mean as a function of sample size have not been discussed previously, and one goal of this paper is to do so in order to provide some insight into the precision of drift sampling.

Inadequate replication in drift studies may be due to the effort usually devoted to frequent sampling over the diel cycle, in order to assess the often dramatic changes in numbers of organisms collected between day and night. If one wishes an absolute estimate of total drift per 24 h, or a detailed description of diel periodicity, it is typical to collect six to eight individual samples over 24 h at 3- to 4-h intervals. In contrast, if drift is measured in order to compare abundances between seasons or sites, it is of primary interest to have replicated estimates of some single measure of drift per site. For this reason, the second goal was to determine whether one can predict the total catch per 24 h from a single sampling interval, thus allowing the effort normally put into frequent sampling over the diel cycle to be put instead into replication of nets.

Methods

Drift was sampled over 4 yr in Cement Creek, Gunnison County, Colorado (see Allan 1975, 1982 for description of area). Nets were placed in the stream at each of three sites about 1 km apart (UC, TR, and LC of Allan 1982) on most sampling dates. On a few occasions only one site (LC) was sampled. The total of 41 collections represented 14 collecting dates ranging from early June to late September. Drift nets had a mouth area of 0.1 m^2, a length of ~2 m, and a mesh size of 0.3 mm. Nets widened ~0.5 m below the opening to minimize turbulence at the net mouth (Waters 1969). The bottom of the net always was >6 cm above the substrate, and the top of the net usually extended above the water surface.

Each drift collection consisted of eight individual samples collected at 3-h intervals over 24 h, in order to quantify diel periodicity in drift activity. The duration of the individual samples ranged from 20 min to 3 h; short sampling duration was necessary during high discharge to avoid net clogging.

Samples were preserved in the field with formalin and rose bengal to facilitate sorting. As some samples contained very large numbers of individuals, we used a plankton splitter to subsample where necessary. Subsamples of 50 or 25% were typical, but occasionally only 12.5% of a sample was counted. Inspection of replicate subsamples (unpubl. data) indicated close correspondence. Taxa abundant enough for statistical analysis included the following: *Baetis bicaudatus*, *Cinygmula* sp., *Epeorus longimanus*, *Drunella coloradensis*, and *Ephemerella infrequens*, Ephemeroptera; *Zapada haysi*, Plecoptera; *Prosimulium* spp. and the Chironomidae, Diptera. The Chironomidae were represented by an unknown number of species, as was the genus *Prosimulium*.

Stream discharge was estimated from measurement of stream width, and triplicate measures of depth and current (using a Pygmy current meter at approximately mid-depth) at each of three points across the stream. Flow through each net was estimated from triplicate readings within the net mouth at the beginning and end of each sampling period, corrected for percent of net mouth submerged.

Quantitative Expression of Invertebrate Drift

The following equations define the several estimates of drift used here, following the recommendations of Waters (1969) and Elliott (1970). First, the number of invertebrates collected per net per hour was estimated from a direct count of the sample, corrected for any deviation in sample duration or in subsampling. Then,

$$(1)\quad \text{Sample drift density} = \frac{\text{numbers per net-hour}}{\text{m}^3\text{ filtered per net-hour}} \times 100$$

where m^3 filtered per net hour is estimated from area of net mouth and current at net mouth. Equation (1) provides a single estimate of numbers drifting per 100 m^3 of water filtered, for an individual hourly sample.

$$(2)\quad \underset{\text{(24HDR)}}{\text{24-h drift rate}} = \frac{3 \times \sum_{i=1}^{8} \text{numbers per net-hour}}{\text{proportion of flow filtered by net}}$$

where proportion of flow filtered by net = flow through net/river discharge, and there are eight sampling intervals per 24 h. Equation (2) estimates the total number of organisms drifting past the sampling point per 24 h.

$$(3)\quad \underset{\text{(24 HDD)}}{\text{24-h drift density}} = \frac{\text{24-h drift rate}}{\text{total stream flow per 24 h}} \times 100.$$

Equation (3) estimates the total 24-h drift per 100 m^3 of water filtered. Waters (1972) has recommended that drift be measured as total quantity of organisms drifting past a point per 24 h, divided by total discharge as a measure of stream size. This has the units numbers $\cdot 24\ h^{-1}$ per $m^3 \cdot s^{-1}$. This differs from equation (3) only by a constant, as Waters' term divided by 864 equals 24HDD. The latter may be preferable because the units of expression are simpler.

Results

Transformation of Estimates of Drift

Many conventional statistical analyses require some transformation of the original data in order to meet the assumptions that the observations are normally distributed with sample variance independent of sample mean (Green 1979). To determine if these drift data required transformation, and which transformations were satisfactory, we used a maximum likelihood method developed by Box and Cox (1964) for locating the optimal transformation. The optimal transformation is given by

$$(4)\quad \begin{aligned} y &= (x^{\lambda} - 1)/\lambda & \lambda &\neq 0 \\ &= \log(x) & \lambda &= 0. \end{aligned}$$

A value of $\lambda = 0$ would indicate a log transformation was preferred, while $\lambda = 0.25$ is the fourth root transformation and $\lambda = 0.50$ is the square root transformation. After the optimal transformation is found, it is possible to test whether each of the three standard transformations is significantly rejected by Chi-square test in comparison with the optimal λ.

We estimated 24HDD at three sites (replicates) on each of 12 collecting dates, and examined these 12 data sets for each taxon to determine the appropriate data transformations. Using the three sites as replicates allows inference about a "typical" stream section in this particular river. One could, depending on the question asked, place three nets within a single section and make statements about the variability within that section, or

TABLE 1. Need for data transformation as examined by the Taylor power law regression (equation (5)) and by the Box–Cox procedure (equation (4)). A significant r^2 indicates that sample variance depended on sample mean. The intercept (a) and slope (b) refer to equation (5). The optimal transformation by the Box–Cox procedure (λ) is compared with three standard transformations by Chi-square test. Underlined Chi-square value indicates which standard transform is closest to optimal, while asterisks indicate rejected transformations ($^*P < 0.05$; $^{**}P < 0.01$).

					Chi-square		
	r^2	a	$b \pm$ 95%CL	λ	$\log x$ ($\lambda = 0$)	$\sqrt[4]{x}$ ($\lambda = 0.25$)	$\sqrt[2]{x}$ ($\lambda = 0.50$)
B. bicaudatus	0.523**	0.629	1.689±1.122	0.242	2.39	0.002	2.80
Cinygmula sp.	0.821**	0.283	1.939±0.631	−0.065	0.63	13.36**	37.43**
E. longimanus[a]	0.739**	0.435	1.425±0.589	0.196	14.50**	1.04	25.05**
D. coloradensis	0.421**	0.481	1.679±1.370	−0.015	0.03	6.57*	20.78**
E. infrequens[a]	0.705**	0.330	1.867±0.830	0.261	3.17	0.005	2.57
Z. haysi	0.406*	0.579	1.630±1.373	−0.009	0.006	3.98*	13.70**
Prosimulium spp.[a]	0.672**	0.565	1.568±0.763	0.251	20.23**	0.001	13.09**
Chironomidae	0.530**	0.876	1.638±1.074	0.313	2.35	0.10	0.89

[a] Data sets contained zeros, so were converted to $(x + 1)$ prior to log transformation.

place one net in each of three nearby rivers and make inferences about rivers in that region. We suspect that our choice of scale probably is of wide application.

The estimate of the optimal transformation ($\hat{\lambda}$) is given in Table 1. The acceptability of various standard transforms is indicated by the Chi-square value (1 df) obtained by testing, via a likelihood ratio test proposed by Box and Cox (1964), each of log, fourth root, and square root against $\hat{\lambda}$. This Chi-square is calculated as $-2 \log_e \gamma$, where γ is obtained by dividing the probability of the observed distributions under various null hypotheses ($\lambda = 0, 0.25, 0.50$) by the probability obtained with the maximum likelihood estimate. The optimal transformation was closest to the fourth root transformation for five taxa, closest to the log transformation for three taxa, and was never closest to the square root transformation (Table 1). However, the log transformation deviated significantly from the optimum for only two of the eight taxa examined, whereas the fourth root transformation deviated significantly from optimal for three of eight taxa.

We also used Taylor's (1961) power law method to investigate the dependency of sample variance on sample mean. For each taxon, the 12 independent estimates of sample variance and sample mean were fit to the equation

$$(5) \quad s^2 = a\bar{x}^b$$

where s^2 = sample variance, $\bar{x}$ = sample mean, and a and b are estimated by linear regression of the log-transformed variables s^2 and $\bar{x}$.

All regressions were significant, with values of b ranging from 1.42 to 1.94. Some 40–82% of the variation in logarithm of variance estimates was accounted for by variation in the logarithm of the means (Table 1).

Precision and 95% Confidence Limits (95%CL)

The 95%CL associated with any sample variance can be determined as a "times–divide factor" (Elliott 1977, p. 90–91) which, multiplied or divided into the back-transformed mean, is similar to a ±CL. For example, a times–divide factor of 1.5 is equivalent to 95%CL ± 50% of the mean. It is calculated from

$$(6) \quad \overset{\times}{\div} \text{ factor} = \text{antilog}\,(t_{0.05}\sqrt{s^2/n})$$

where s^2 = sample variance computed from log-transformed data, n = number of replicates per sample, and $t_{0.05}$ = tabulated value from Student's t-distribution with $n - 1$ degrees of freedom. In order to employ the times–divide factor, the logarithmic transformation must be used.

Sample variances were computed for log-transformed 24HDD estimates for the abundant mayfly *B. bicaudatus* on each of 12 dates (n = 3 replicates per date, data of Table 1). We then estimated 95%CL as a function of number of replicates n, and because true sample variance (σ^2) usually is unknown, we chose several representative values of s^2 as estimates of σ^2. As

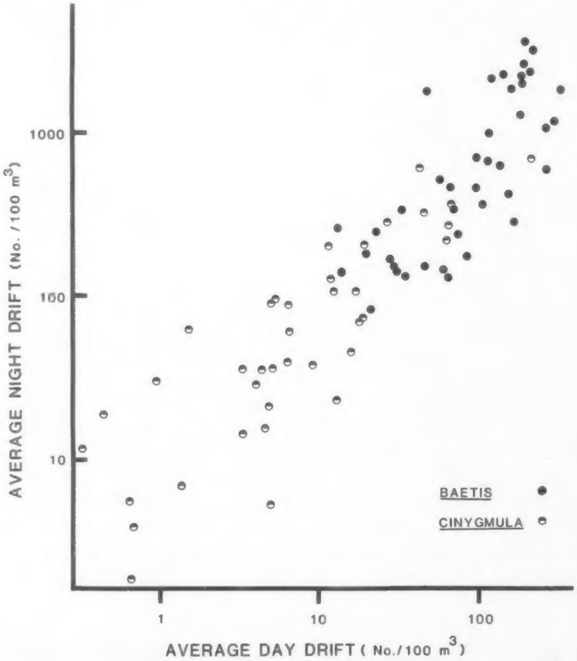

FIG. 1. Association between average day drift and average night drift for *B. bicaudatus* and *Cinygmula*.

TABLE 2. Proportion of variation accounted for (r^2) and coefficients (a, b) from regression analyses of drift density. The first variable listed is the dependent variable. All regressions were significant. With 10 df, $r^2 > 0.33$ is significant at 0.05, $r^2 > 0.50$ is significant at 0.01 level.

	Average night drift with average day drift			First night drift sample with remaining 7 samples		
	r^2	a	b	r^2	a	b
B. bicaudatus[a]	0.634	0.154	1.581	0.711	−0.885	0.260
Cinygmula sp.[b]	0.729	0.670	1.044	0.724	0.579	0.156
E. longimanus[a]	0.616	0.598	1.098	0.765	0.286	0.213
E. coloradensis[b]	0.331	0.298	1.164	0.692	0.120	0.313
E. infrequens[a]	0.449	0.454	1.160	0.609	−0.186	0.237
Z. haysi[b]	0.694	0.713	0.988	0.710	0.517	0.152
Prosimulium[a]	0.802	0.314	1.135	0.897	0.014	0.186
Chironomidae[a]	0.793	0.234	0.961	0.801	0.336	0.150

[a] Fourth root transformation.

[b] Logarithmic transformation.

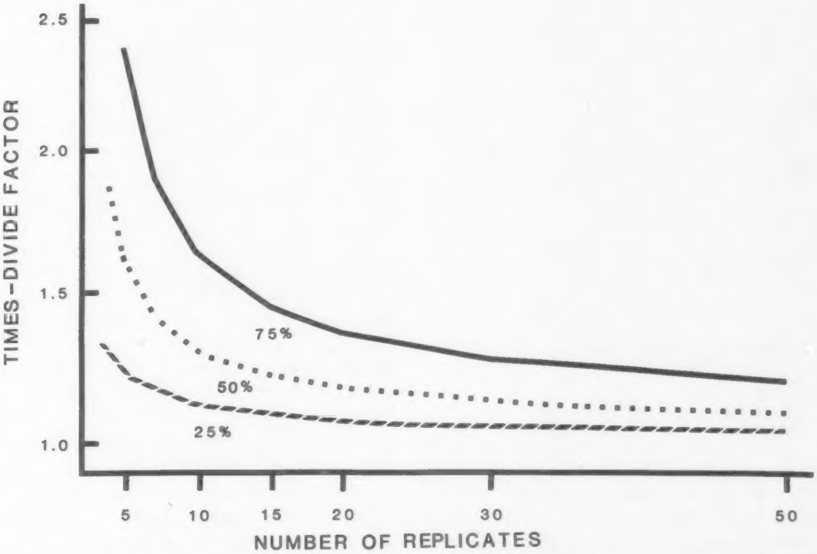

FIG. 2. The 95%CL of estimated drift density of *B. bicaudatus* expressed as a multiple of the mean (times–divide factor), as a function of number of replicate samples. Of 41 collections, 25% had variances resulting in a times–divide factor as small or smaller than the lowest curve. Half the data sets had variances that would result in times–divide factors as small or smaller than the 50% curve, while one quarter of the data sets had variances that would result in a times–divide factor greater than the 75% curve.

expected, 95%CL declined rapidly, then more slowly, with increasing n (Fig. 1). Some 25% of the 12 data sets had variances less than or equal to the value producing the lowest line in Fig. 1. The next largest 25% of variance estimates resulted in CL between the bottom and middle curves. The next largest 25% of variance estimates resulted in CL between the middle and upper curves, while 25% of the data sets result in CL larger than those indicated by the top line.

Estimating Drift from a Single Sample

For a reasonable estimate of total drift from a single sample, day and night drift should be highly correlated. We regressed average day drift, computed from four samples during the day, on average night drift, computed from three samples during the night, using sample drift density (equation (1)) and either the log or fourth root transformation, depending upon the taxon (Table 1). Some 33–80% of the variation in average night drift density was explainable by variation in average day drift density. Both *E. infrequens* and *D. coloradensis* showed low correlations, while in the other six taxa the coefficient of determination was >0.62 (Table 2).

The correspondence between night and day drift is depicted graphically for *B. bicaudatus* and *Cinygmula* (Fig. 2). There was a tendency for scatter to increase at low drift densities. The range of values was less for some taxa (e.g. the Chironomidae) than for others (e.g. *B. bicaudatus*), which may account in part for observed differences in strength of correlation (Table 2).

Finally, we regressed drift density from the first night collection against drift density of the remaining seven samples from each 24-h period to determine how well a single sample predicted the information that would be lost if complete diel sampling was omitted. As 60–90% of the variation in estimates of drift from seven of the diel samples was accounted for by variation in the single sample collected just after dark (Table 2), it is clear that 24-h drift is predicted well by sampling only once in the 24-h period.

Discussion

For each of the eight taxa examined, a transformation was required to normalize the data and reduce the dependency of sample variance on sample mean. Values of b from Taylor's power law (equation (5)) suggest a fourth root transformation if $b = 1.5$, and a log transformation if $b = 2$. With the possible exception of two taxa (*Cinygmula* and *E. infrequens*), from the results of Table 1 we suggest that the fourth root should be a good general transformation for drift data. However, log transformation eliminated any significant dependence of sample variance on sample mean for each of the eight taxa (unpubl. analysis). The Box–Cox procedure gave broadly similar results (Table 1); the log transformation was significantly worse than the optimal for two taxa, while the fourth root was significantly worse than optimal for three taxa.

Reducing the dependency of variance on the mean (Taylor 1961) is one approach to meeting the assumptions of analyses of variance. However, fitting equation (5) requires several samples in order to compute an adequate regression equation. The approach of Box and Cox (1964) can be employed with a smaller number of samples (even one if replicate × treatment degrees of freedom are adequate, approximately $>20–30$). Either transformation will improve the performance of subsequent analyses if data initially are skewed (Scheffé 1959), and a transformation is especially needed if multiple comparison procedures are to be employed.

Clearly, one cannot generalize about the adequacy of a single transformation to normalize data and reduce the dependence of the variance on the mean in every instance, although it may be that either the log or fourth root transformation usually will be successful. For a data set that includes a number of taxa, it may be desirable to employ the same transformation for all, using the best common or closest standard transformation, provided that whichever transformation one chooses is not strongly counterindicated for some taxon. Finally, there may be other reasons for choosing a particular transformation; for instance, the times–divide approach to 95%CL requires log transformation of the data.

Analysis of the precision of replicate estimates of 24HDD, expressed as a times–divide factor, showed that sample variance itself is variable (see the family of curves in Fig. 1). With only one or two samples, there is little reason to believe that estimated drift density is within 100–200% of its true value. Some six to seven replicates are required, based on the data for a single, abundant species (*B. bicaudatus*), to expect 95%CL on drift to fall within ±50% of the mean.

This appears to be somewhat better precision than benthic samples provide. Using replicate Surber samples from the same stream, Allan (1984) estimated 95%CL using the average variance obtained for *B. bicaudatus*. Five benthic samples resulted in 95%CL of at least ±130–150% of the mean, and 10–15 benthic samples would be needed to achieve the same precision obtained with 5 drift samples. This agrees with Chutter's (1975) conclusion that for the same number of replicates, drift samples are more precise than benthic samples.

Since it is common for studies of drift to utilize six or eight samples spread over a 24-h period to obtain a single summed estimate of drift density or rate, replicating the entire effort six times at perhaps two sites (for comparative purposes) becomes a formidable undertaking. This was the basis for investigating the correlation between day and night drift, in order to justify using a single sampling period as a predictor of 24-h drift. The first night sample, which typically is the largest of the 24-h series, provided most of the information (60–90%, Table 2) available in the remaining seven samples. Wherever the purpose of the investigation is to compare drift densities in stream sections exposed to various experimental or natural treatments, rather than estimate absolute numbers drifting per 24 h, we consider that effort would be better invested in some number of replicated samples collected just after nightfall, rather than an unreplicated series of collections spread over 24 h.

This recommendation assumes that one cannot simply leave a net in place continuously for 24 h. Although in some instances, one can (Waters 1969), the quantity of drifting insects and debris often precludes this possibility, and necessitates a choice between repeated sampling over 24 h and replicated sampling at a single time. Thus, for many questions concerning comparisons, we suggest it is preferable, for the same effort, to know the precision of an estimate at a single time rather than to estimate diel periodicity with unknown precision. Because most taxa exhibit peak drift just after dark, that is the best single time to sample.

The strong correlation between day and night drift may also have some bearing on the ideas of constant drift, which refers to the low level of drift usually observed during the day, and behavioral drift, which refers to the typically large increase in drift that occurs at night (Waters 1965). Based on these categorizations, one might expect that night (= behavioral) might be a very poor predictor of day (= constant) drift. Clearly, day and night drift are related, however, and the relationship was significant after the effects of benthic density and discharge were removed by partial correlation analysis (J.D. Allan, unpubl. data). This may indicate that day drift should not be viewed as an accidental event completely unrelated to the behavior that results in large peaks in night drift, but perhaps reflects incomplete suppression of the identical behaviors.

Acknowledgments

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Wound Healing in the Bottlenose Dolphin (*Tursiops truncatus*)

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Bruce-Allen, L. J., and J. R. Geraci. 1985. Wound healing in the bottlenose dolphin (*Tursiops truncatus*). Can. J. Fish. Aquat. Sci. 42: 216–228.

Early stages of wound healing were characterized in three bottlenose dolphins (*Tursiops truncatus*). A total of six 10-cm-long, 2-mm-deep incisions into the dermis were infused with sterile seawater for 30 min. Biopsies representing all surfaces of the cuts were taken at 2, 6, and 12 h and 1, 2, 3, 7, and 10 d. Histologically, wounds from 6 through 72 h were characterized by a mixed cell infiltrate predominated by neutrophils, and extensive areas of intraepidermal vesicles. Migrating epidermal cells bridged the incisional gap by 2 d, while elevated mitotic activity of basal cells restored full epidermal thickness by day 7. Notable was the absence of a traditional scab; its purpose was served by a transformed barrier layer of epidermal cells and vesicles. As well, an abnormal intracellular distribution of melanosomes typified new epidermal cells. The sequence and timing of healing in *Tursiops* are similar to those reported in terrestrial mammals; differences in the appearance of healing are most likely due to adaptations to an aquatic lifestyle.

Les premiers stades de cicatrisation des blessures ont été décrits chez trois dauphins à gros nez (*Tursiops truncatus*). On a baigné avec de l'eau de mer stérile pendant 30 min. Six incisions longues de 10 cm et profondes de 2 mm pratiquées dans le derme. Des tissues représentant toutes les surfaces des coupures ont été prélevés toutes les 2, 6 et 12 h ainsi que tous les 1, 2, 3, 7 et 10 jours. Sur le plan histologique, les blessures remontant de 6 à 72 h étaient caractérisées par une infiltration de cellules mélangées constituées surtout de neutrophiles et par de vastes régions marquées de vésicules intraépidermiques. Des cellules épidermiques sont venues recouvrir l'ouverture de l'incision vers le 2^e jour, tandis que l'activité mitotique élevée des cellules basales reconstituait toute l'épaisseur de l'épiderme vers le 7^e jour. Fait à noter, la croûte traditionnelle était absente ; son rôle était rempli plutôt par une couche protectrice transformée de cellules et vésicules épidermiques. Par ailleurs, une distribution anormale de mélanosomes à l'intérieur des cellules caractérisait les nouvelles cellules épidermiques. Le déroulement et la durée de la cicatrisation chez *Tursiops* sont semblables à ceux signalés chez les mammifères terrestres ; les différences d'aspect de la cicatrisation sont fort probablement dues à des adaptations à un mode de vie aquatique.

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Cetacean skin is smooth, taut, and hairless and departs from typical mammalian design in its lack of cutaneous appendages and glands. The foundation consists of prominent dermal ridges which run along the long axis of the body and penetrate up to one-half the thickness of the epidermis as dermal papillae (Sokolov 1960). The papillae are richly supplied with blood, and with end organs that morphologically resemble Vater–Pacini corpuscles (Palmer and Weddell 1964). The epidermis has three distinct strata (Sokolov and Kalashnikova 1971). The deepest, or stratum germinativum, is composed of a single layer of mitotically active columnar cells interspersed with melanocytes. The germinal cells gradually transform and enter the overlying stratum spinosum, the thickest layer of cetacean epidermis. They eventually flatten and undergo degenerative changes as they approach the surface to become compressed into a distinct band, known as the stratum externum, which in *Tursiops* is 10–15 cell layers thick (Harrison and Thurley 1974). The cells of this outermost layer are incompletely keratinized (Spearman 1972).

Inherent differences in cetacean skin have led to some extraordinary claims regarding its nature and function. Still unsubstantiated are the claims that the skin may serve an osmotic function (Viale 1979; Hui 1981), proliferates at a remarkably fast rate (Palmer and Weddell 1964), and as a natural consequence, heals more rapidly than in terrestrial mammals (Greenwood et al. 1974).

We approached the latter question by undertaking a basic study to characterize the acute inflammatory response and wound healing in the bottlenose dolphin, *Tursiops truncatus*, focusing on the role of inflammatory cells, the sequence of degenerative and regenerative changes, and the rate at which these events occur.

Materials and Methods

Three 4-yr-old female bottlenose dolphins were captured in the Mississippi delta and maintained in sea-pen enclosures at the Institute for Delphinid Research, Grassy Key, FL, for 16 mo prior to the study. Each dolphin was fed herring (*Clupea harengus*) and smelt (*Osmerus mordax*), providing a daily ration of 0.34×10^6 J·kg body weight^{-1}·d^{-1}.

During the 7-mo study period, the animals were in good health, judging from appetite, general appearance, and results of hematologic and blood chemical parameters.

For each trial, the dolphins were netted, placed on a standard dolphin transport stretcher, and suspended side-by-side just above the surface of the water on a metal carrier frame. The animals were restrained for up to 3 h while being kept moist by sponging. Following each session, the dolphins were fed as soon as they were returned to the holding pool.

We examined the healing process by making two 10-cm-long superficial cuts on the back of each animal. A sterilized No. 11 scalpel blade, wrapped with masking tape as a depth gauge, so that 2 mm of the tip was exposed, was drawn quickly through the full 1.5-mm thickness of epidermis and into the dermis. A paper ruler, placed cranial and at right angles to the dorsal fin, was used to guide the blade. Bleeding was controlled within 2 min using a gauze sponge, after which each cut was infused with sterile seawater for 30 min.

The cuts were photographed and elliptical skin biopsy specimens were excised in duplicate at 2, 6, and 12 h and 1, 2, 3, 7, and 10 d after each cut was made. They were removed serially beginning at one end of the incision. Each specimen exposed the dermis and incorporated the opposing edges of the wound and normal surrounding tissue.

Samples were placed immediately in 4 mL of 3% glutaraldehyde in 10% buffered formalin (0.2 M sodium phosphate buffer (M = mol/L), pH 7.0), at 4°C for up to 1 h. Each specimen was then bisected longitudinally, one half was placed in 4 mL of fresh glutaraldehyde–formalin fixative for light microscopy, and the other was diced into 1-mm^3 pieces and placed in 4 mL of the same fixative for electron microscopy.

Tissues fixed for light microscopy were dehydrated in alcohol, xylene, and embedded in paraffin blocks. Sections 10–12 μm thick were stained with hematoxylin and eosin (H&E). Selected subsamples from each time interval were stained with periodic acid schiff (PAS), phosphotungstic acid hematoxylin (PTAH), and Masson's trichrome.

For electron microscopy, specimens were postfixed in 1% osmium tetroxide in 0.2 M sodium phosphate buffer for 1 h at 4°C. They were then washed in 0.2 M sodium phosphate buffer, dehydrated in acetone, and embedded in Spurr's medium. Thick sections (1 μm) were cut on glass knives using a Reichert OmU$_2$ ultramicrotome (Sargent-Welch Scientific of Canada Ltd., Weston, Ont.) and stained with 1% methylene blue in 1% sodium borate solution at 90°C for 1 min. Thin sections (150 nm) were placed on 200-mesh copper–nickel grids and stained with 2% uranyl acetate in water for 20 min and lead citrate for 5 min. Thin sections were viewed on an Hitachi HS-9 electron microscope (Nissei Sangyo Canada Ltd., Rexdale, Ont.).

Inflammatory cells located at the base of the incision were identified in H&E stained sections as neutrophils, eosinophils, or mononuclear cells using oil immersion (1000×). Each of the three cell types was counted in six random 2.0×10^{-3} mm^2 fields on three histological sections using a gridded ocular. The mean and standard deviation of the six counts were calculated to yield a value for the density of each inflammatory cell type. Mitotic activity of germinal cells was determined by counting cells in metaphase within 2 mm (containing approximately 500 cells) of the incision line.

Results

Application of gauze pads to minimize bleeding was effective usually within 2–3 min. Bleeding could be induced again by gently massaging the cut during the next 2 h but not thereafter.

2 Hours

Cuts examined after 30 min and 2 h showed sharp clean edges separated by a space approximately 2 mm wide (Fig. 1B). After 2 h the incisions were filled with coagulated blood. Histologically, the coagulum was composed of erythrocytes and strands of fibrin. Epidermal cells from the margins of the incision inward to a depth of up to 0.2 mm at the base and 1.0 mm at the surface were pale, had pyknotic nuclei, and lacked distinct cell architecture (Fig. 1C). At the base of the incisions, mild intercellular edema was evident in the stratum germinativum and the first few layers of the stratum spinosum. Small blood vessels in the peri-incisional dermis were dilated and congested (Fig. 1D). The endothelial cells were fusiform and contained numerous peripheral vesicles. Erythrocytes and a few neutrophils were commonly encountered adhering to the walls of the vessels. Neutrophils were identified as round to ovoid cells, 5–10 μm in diameter, containing polysegmented nuclei and two species of cytoplasmic granules. The cells often possessed cytoplasmic extensions devoid of organelles.

6 Hours

There was little change in the gross appearance of the cuts after 6 h. They remained clean and exhibited raised, sharp black edges (Fig. 2B) which were marginally retracted, increasing the incisional gap to slightly over 2 mm. Coagulated blood was visible in the incisions, but there was no evidence of fresh bleeding even after vigorous handling.

Histologically, a more mature fibrinous exudate formed of lysed erythrocytes, fibrin, and neutrophils filled the entire incisional gap (Fig. 2C). A mixed cell infiltrate was present in the dermis at the base of the incisions. The average density of inflammatory cells was 10^4 cells$\cdot$mm^{-2}, of which 90% were neutrophils and the remaining were eosinophils and mononuclear cells. Eosinophils were characterized by monotypic large homogeneous granules (Fig. 2D) which often covered the polysegmented nucleus. Mononuclear cells possessed unsegmented nuclei, rough endoplasmic reticulum, and uniformly small cytoplasmic granules (Fig. 2D).

Most noticeable in 6-h specimens was a marked increase in intercellular edema adjacent to and extending approximately 50 μm on either side of the incision (Fig. 2C). Channels of edema often coalesced forming small vesicles within and directly beneath the layer of degenerating cells bordering the incision. This resulted in the rupturing of desmosomal attachments, and filling of intercellular spaces with PAS-positive material, cell debris, and cellular infiltrate predominated by neutrophils (Fig. 2C). The basement membrane along 0.5 mm on either side of the incision was somewhat thickened and was often bridged to the dermis with fibrillar material.

Ultrastructural examination of inflammatory cells showed the neutrophils to be phagocytic. The cells often bore pseudopodia in the process of enclosing minute quantities of the surrounding medium, and phagosomes containing debris and proteinaceous matter. Ultrastructural changes were also evident in the endothelial cells of the vessel walls. The perinuclear and nuclear areas of the cells appeared more circular and extended both into the lumen of the vessels and into the dermis.

12 Hours

At 12 h, all the cuts were clean. The edges were dark, slightly rounded and raised, with no further retraction beyond that

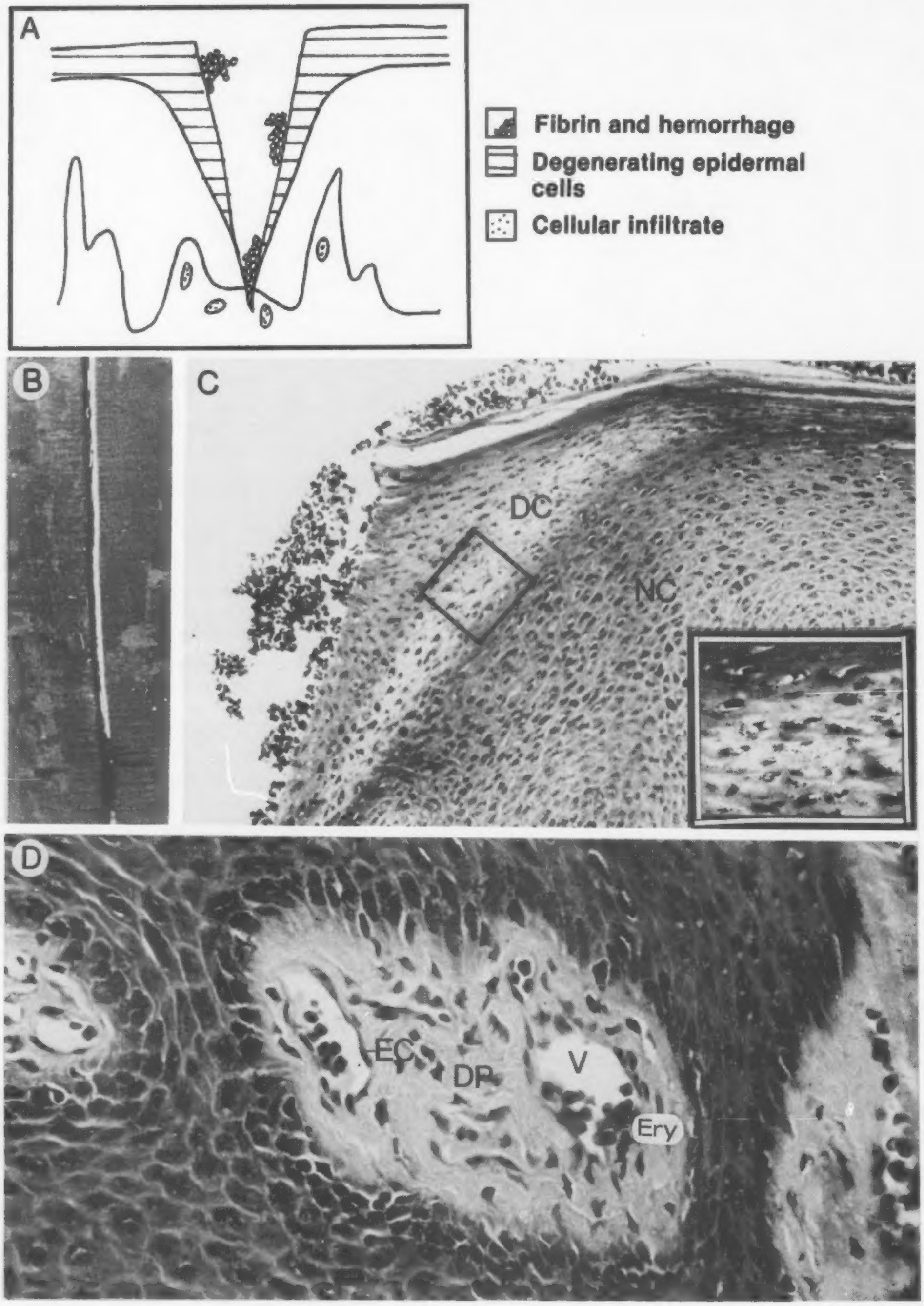
A
Fibrin and hemorrhage
Degenerating epidermal cells
Cellular infiltrate
B
C
DC
NC
D
EC
DP
V
Ery

FIG. 1. (A) Schematic representation of cut at 2 h. (B) Renewed bleeding of cut following movement of dolphin. (C) Layer of pale, degenerating epidermal cells (DC) lining margins of cut; NC, normal cells (H&E, ×400). Inset: nuclear and cytoplasmic changes in degenerating cells (H&E, ×429). (D) Congested dilated vessels (V) in dermal papilla (DP) adjacent to cut. EC endothelial cell; Ery, erythrocyte (H&E, ×1179).

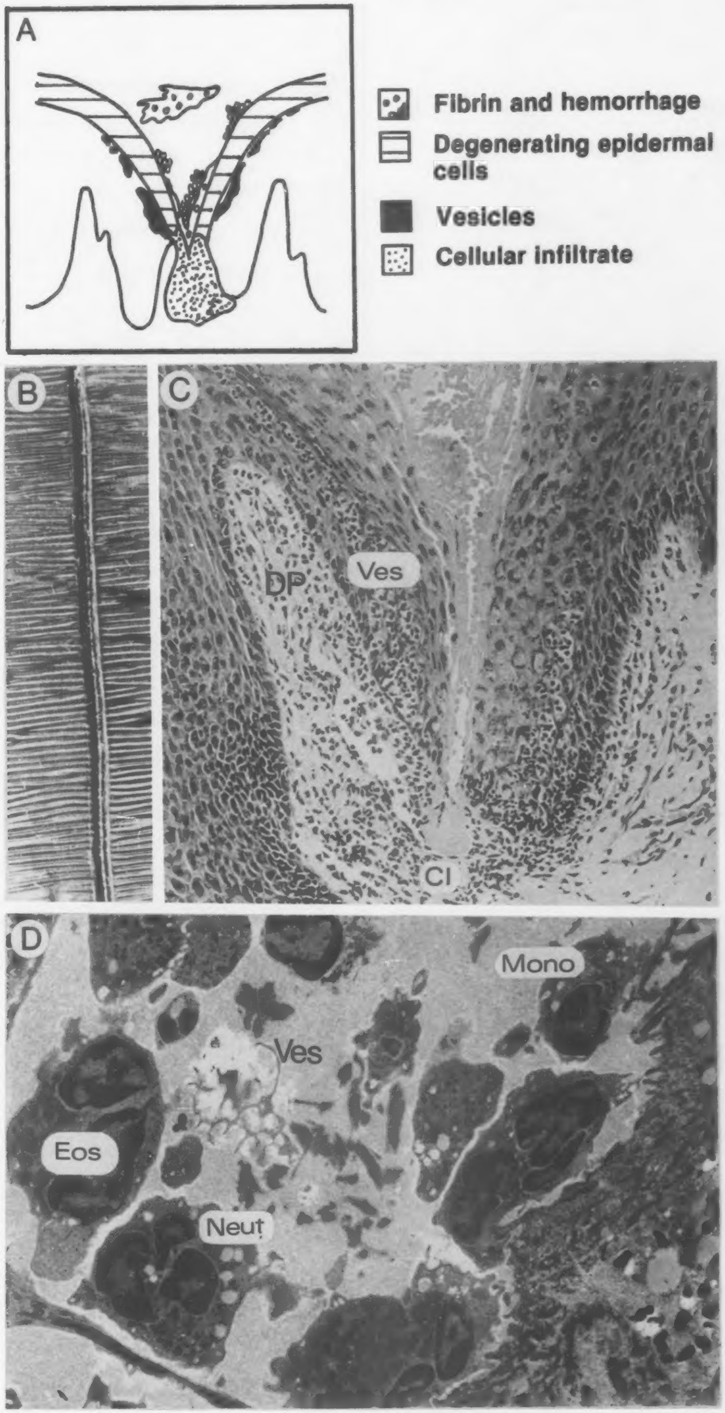
A
Fibrin and hemorrhage
Degenerating epidermal cells
Vesicles
Cellular infiltrate
B
C
DP
Ves
CI
D
Mono
Ves
Eos
Neut

FIG. 2. (A) Schematic representation of cut at 6 h. (B) Clean, black, slightly raised edges of cut. (C) Cell infiltrate (CI) present at base of cut and dermal papilla (DP), and small vesicles (Ves) formed by intercellular edema and infiltration of neutrophils (H&E, ×443), (D) Neutrophil (Neut), eosinophil (Eos), and a mononuclear cell (Mono) in a vesicle at base of cut (×5063).

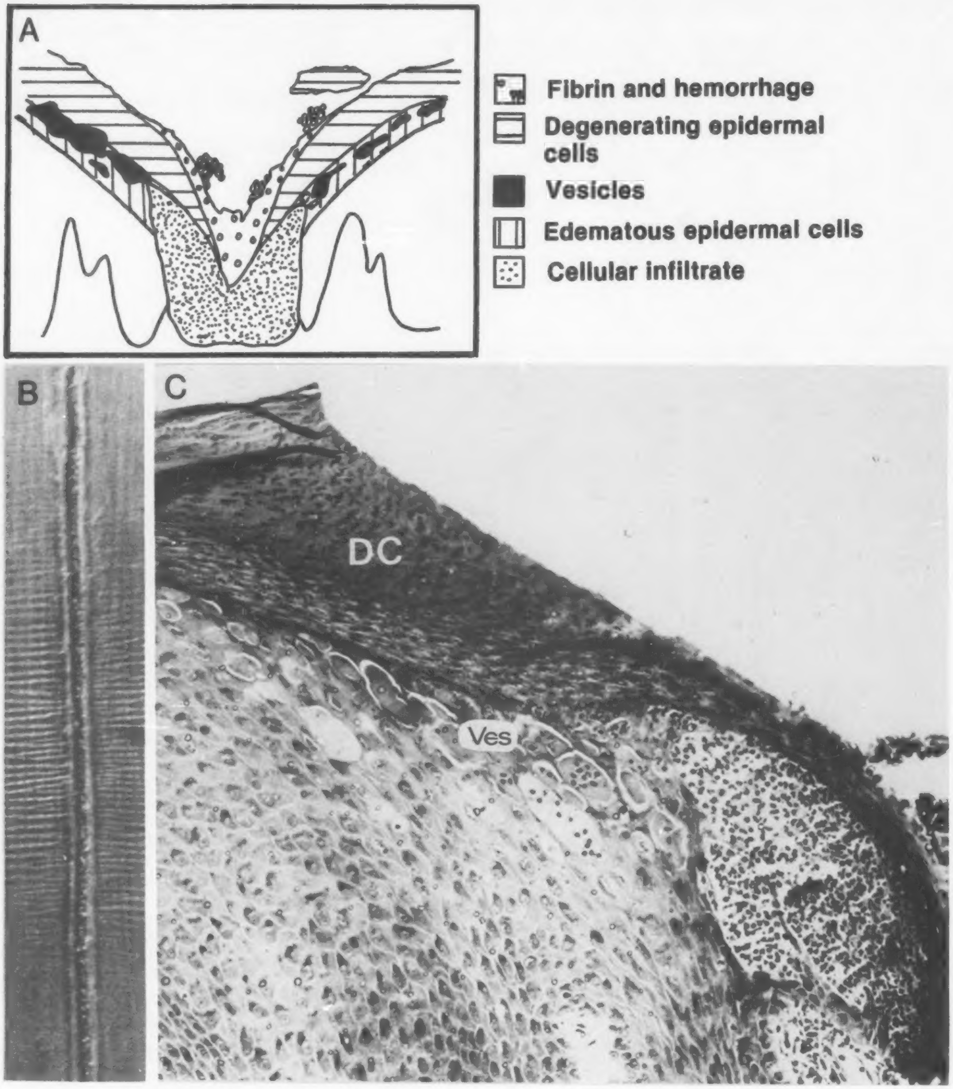

FIG. 3. (A) Schematic representation of cut at 12 h. (B) Raised edges of cut bordered by narrow dark grey band. (C) Coalescent serum and neutrophil-filled vesicles (Ves) beneath layer of degenerating epidermal cells (DC) (H&E, ×486).

observed at 6 h (Fig. 3B). Histologically, approximately two thirds of the layer of degenerating epidermal cells lining the incision had exfoliated, and that which remained was bordered by the extensive area of vesicles (Fig. 3C).

Epidermal cells forming the inner edges of the incision at the base became elongated and projected cytoplasmic extensions into the underlying dermis. The basement membrane extending up to 1.0 mm on either side of the incision beneath these cells was thickened. The density of the cell infiltrate at the base of the cuts was 3×10^4 cells·mm^{-2}. In both the vesicles and peri-incisional dermis, the infiltrate was, as in the 6-h specimen, composed of 90% neutrophils and the rest mononuclear cells and eosinophils. Most cells were phagocytic. Futhermore, many neutrophils contained karyorrhectic or pyknotic nuclei, large or numerous small phagolysosomes, and granule-depleted cytoplasm. Mononuclear cells, however, appeared healthy, exhibiting normal nuclei and granules, despite the presence of phagosomes.

1 Day

After 1 d, the edges of the incisions were closely opposed, slightly swollen, pale grey ridges which obscured the base of the cuts (Fig. 4B). The shoulders of the incisions had a spongy texture and were surrounded by a sharp black line. Histologically, most of the degenerating epidermal cells, and some of the vesicles that had been lining the incisional edges in early samples, had now exfoliated. Small vesicles were loosely held together and their necrotic contents were released into the remaining layer of degenerating cells and the lumen of the cut

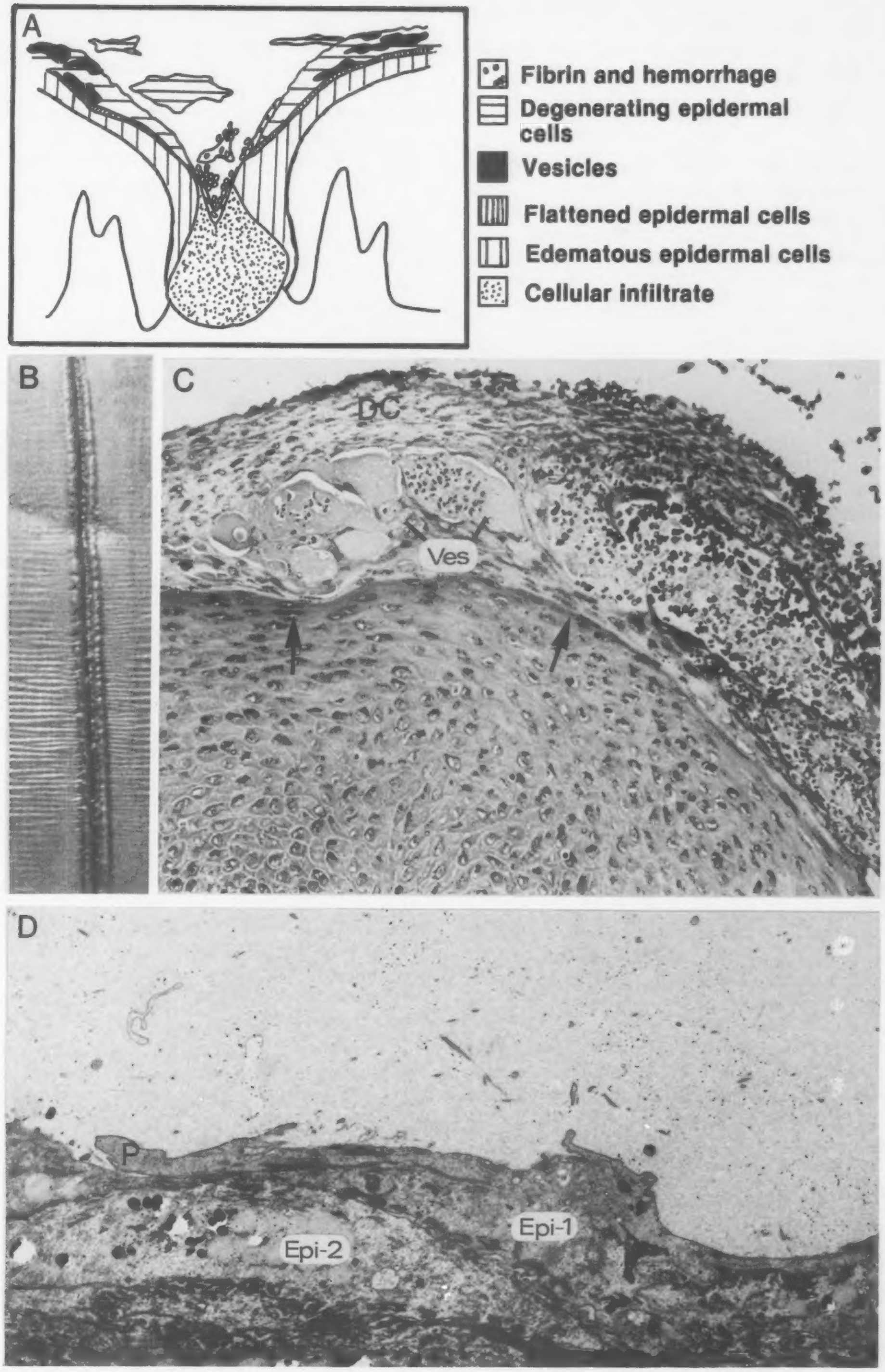
A
Fibrin and hemorrhage
Degenerating epidermal cells
Vesicles
Flattened epidermal cells
Edematous epidermal cells
Cellular infiltrate
B
C
DC
Ves
D
P
Epi-2
Epi-1

FIG. 4. (A) Schematic representation of cut after 1 d. (B) Raised, spongy edges of cut bordered by dark grey band. (C) Vesicles (Ves) within exfoliating degenerating epidermal layer (DC); degenerating layer is bordered by flattened spinous cells (arrows) resembling stratum externum (H&E, ×457). (D) Migrating epidermal cell (Epi-1) extends pseudopod (P) over stationary epidermal cell (Epi-2) (×5375).

which still contained an abundant hemorrhagic exudate. One or two layers of viable cells of the stratum spinosum underlying the remaining vesiculated areas appeared flattened, oriented in a plane parallel to the surface of the skin, and possessed condensed nuclei (Fig. 4C), thus resembling cells of the stratum externum.

Pseudopod-bearing epidermal cells at the base of the incision extended and migrated along the deepithelialized dermis (Fig. 4D) to fill the gap in the skin caused by the cut. The basement membrane beneath these cells remained two to three times thicker than normal. The mean density of inflammatory cells at the base of the cuts after 1 d was 2.7×10^4 cells$\cdot$mm^{-2}, composed of approximately 85% neutrophils and occasional mononuclear cells and eosinophils.

2 Days

Following 2 d, the edges of the incisions were slightly puckered and bordered laterally by a 1-cm-wide dark grey halo (Fig. 5B). The layer of degenerated cells and vesicles bordering the incision had completely exfoliated, exposing a stratum-externum-like layer composed of 5–10 layers of flattened, elongated cells containing nuclei undergoing pyknotic changes. Beneath this lay a pocket of enlarged spinous cells containing a frothy cytoplasm interspersed with inflamatory cells (Fig. 5C). Ultrastructural examination of the spinous cells indicated that the increase in cell size was associated with intracellular edema accompanied by peripheral clumping of nuclear chromatin and aggregation of tonofilaments (Fig. 5D). Directly below this pocket extended a narrow column of nonaligned spinous cells with clear nuclear haloes, and diffuse melanosomes (Fig. 5C). Migration of basal epidermal cells was complete between 24 and 48 h. The foundations of the new epidermis were thus established from which three epidermal strata, stratum germinativum, an extensive stratum spinosum, and a thin stratum externum, developed by 48 h. Mitotically active epidermal cells were observed in the stratum germinativum up to 1 mm on either side of the cuts. The mitotic activity of the peri-incisional area of these specimens was approximately four times that of previous specimens (Table 1). The basement membrane underlying the epidermis was indistinguishable from the membrane far removed from the site of the incision. However, dermal papillae, which normally extend into the epidermis, were absent beneath the incision.

Inflammatory cells were confined to a small pocket or band in the dermis beneath the base of each cut. The infiltrates were composed of approximately 80% neutrophils, most of which had pyknotic nuclei and a pale-staining homogeneous cytoplasm.

Ultrastructurally, the blood vessels in the peri-incisional dermis appeared normal. The lumens of the vessels contained three to four erythrocytes, and the endothelial cells resumed their normal fusiform appearance.

3 Days

Following 3 d, the cuts were visible as shallow depressions in the skin (Fig. 6B). There was a 2-mm-wide gap between the puckered edges; the trough had a slightly roughened appearance.

Light microscopy revealed nearly complete reestablishment of normal epidermal structure (Fig. 6C). Elongated epidermal cells with condensed nuclei formed a continuous layer across the incisional gap. There yet remained a mild reduction in thickness of the epidermis. Pale swollen cells lined the depression left by the incision and extended four to five cell layers into the spinosum. Beneath this pocket of degenerating cells were 10–20 layers of edematous cells, overlying approximately 10 layers of healthy spinosum cells. Mitotic activity of basal cells within 1 mm of the cut was eight times that of the control (Table 1). Occasional inflammatory cells, predominantly neutrophils, were confined to a narrow band at the dermal–epidermal junction beneath the injured area. As observed in 2-d-old specimens, dermal papillae were absent in the peri-incisional area.

7 Days

After 7 d, the cuts were closed but visible as white linear marks (Fig. 7B). A 0.5-cm-wide medium grey halo remained around the scars and gradually blended with the surrounding tissue. Histologically, full epidermal thickness was restored (Fig. 7C). However, in 75% of the specimens, the surface of the epidermis at the former sites of the cuts was ragged or torn. This was undoubtedly an artifact of handling, yet it points to the fragility of the newly repaired wound site. Beneath the externum there remained one to two layers of enlarged, edematous spinous cells (Fig. 7C). Extending from these cells downward to the stratum germinativum was a narrow column, approximately 1 mm wide, of pale unaligned spinous cells with a diffuse distribution of melanosomes. The mitotic rate of germinal epidermal cells remained approximately seven times that of controls (Table 1) and was confined to a single layer within 1 mm of the cuts. The dermis beneath the wound site was completely restored with dermal papillae extending uniformly into the epidermis. A slight neutrophilic infiltrate remained as a narrow band at the dermal–epidermal junction beneath the cuts.

10 Days

A 0.5-cm-wide white linear mark bordered by a narrow dark grey band was all that remained of the cuts after 10 d (Fig. 8B). Histologically, the only evidence of the cuts was a 0.5-mm-wide column of pale, unaligned spinous cells extending approximately half the thickness of the epidermis (Fig. 8C). Similar to specimens removed after 7 d, the surface of the epidermis overlying the former cuts was often artifactually torn. The mitotic rate of specimens decreased to 3.4 cells$\cdot$1000^{-1} (Table 1), slightly above control values.

TABLE 1. Mitotic activity of the stratum germinativum within 2 mm of incisions in the skin of *Tursiops truncatus*.

Time after incision	Mean number of cells in metaphase per 1000 basal cells[a]	Standard deviation
Control[b]	1.2	0.52
2 h	1.2	0.52
6 h	1.0	0.53
12 h	1.2	0.70
1 d	1.4	0.67
2 d	5.4	1.16
3 d	9.6	1.50
7 d	8.6[c]	0.96
10 d	3.4[c]	0.79

[a] 500 basal cells were counted on each of 10 biopsy specimens.

[b] Biopsy specimen removed from nonincisional area.

[c] 500 basal cells were counted on each of 4 biopsy specimens.

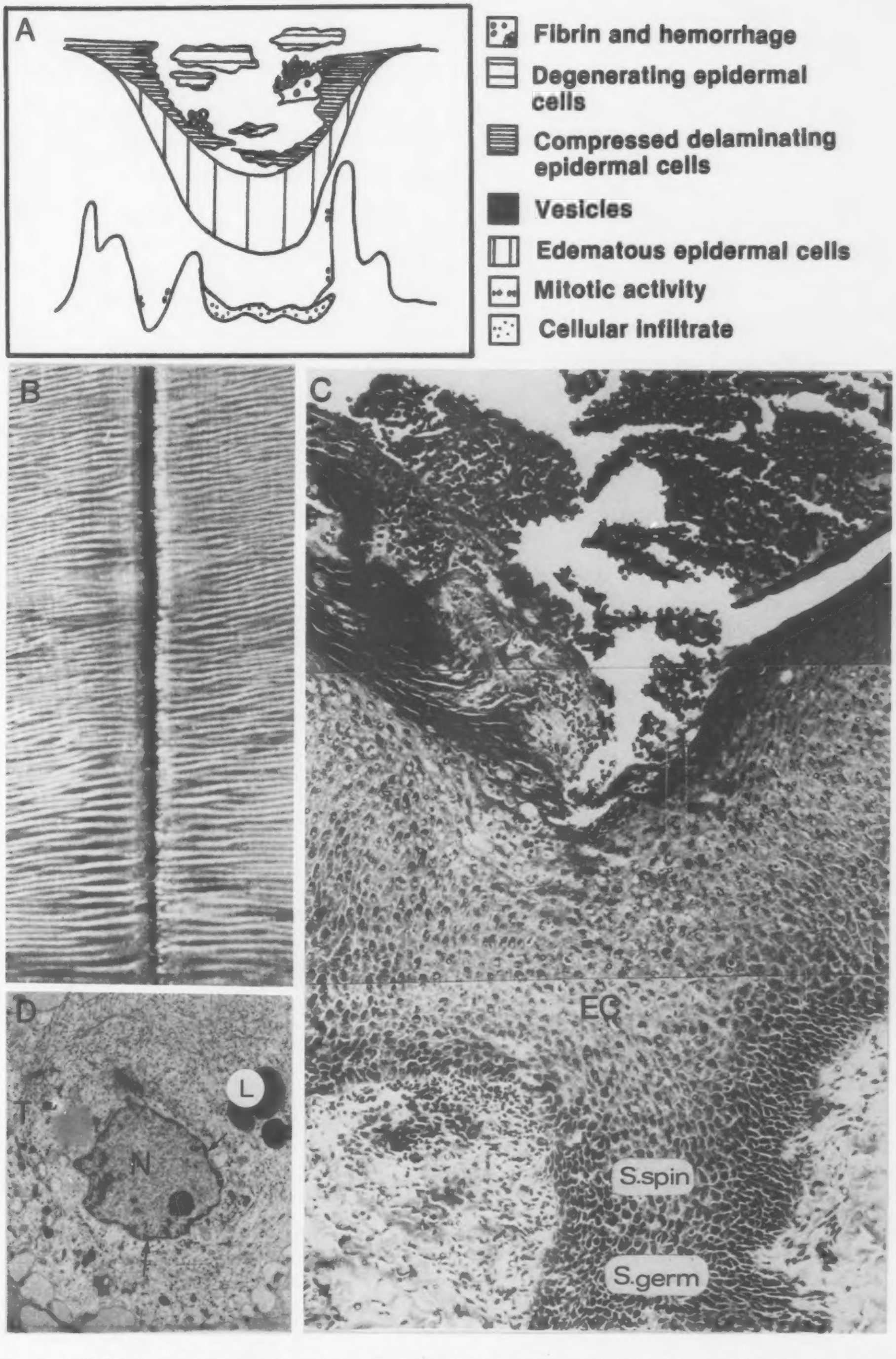
A
Fibrin and hemorrhage
Degenerating epidermal cells
Compressed delaminating epidermal cells
Vesicles
Edematous epidermal cells
Mitotic activity
Cellular infiltrate
B
C
EC
S.spin
S.germ
D
L
T
N

FIG. 5. (A) Schematic representation of cut after 2 d. (B) Slightly puckered edges of cut bordered by darker grey band. (C) Reestablished stratum germinativum (S. germ) and stratum spinosum (S. spin); approximately 75% of the epidermal cells (EC) filling in the wound are enlarged and edematous (H&E, ×314). (D) Edematous cell has normal lipid droplets (L), aggregated tonofilaments (T), and nucleus (N) with peripherally clumped chromatin (arrows) (×3000).

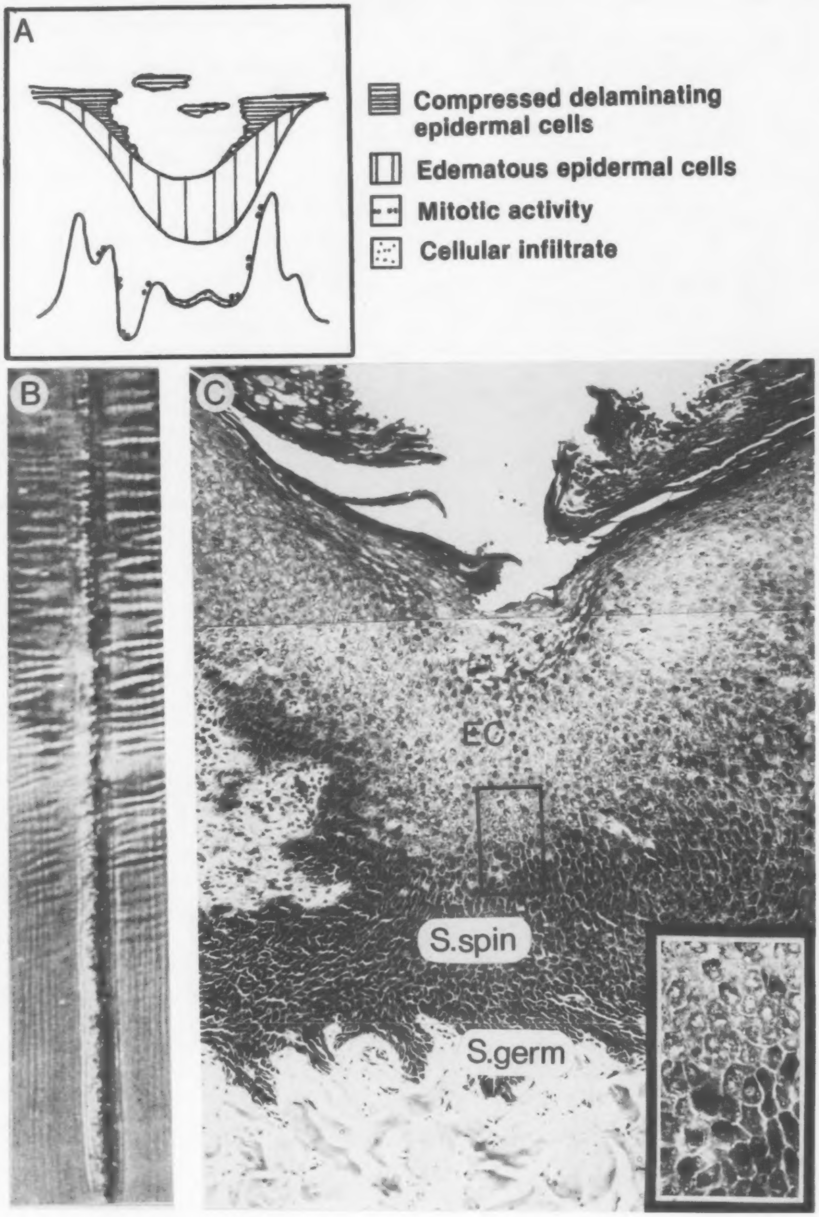
A
Compressed delaminating epidermal cells
Edematous epidermal cells
Mitotic activity
Cellular infiltrate
B
C
EC
S.spin
S.germ

FIG. 6. (A) Schematic representation of cut after 3 d. (B) Epidermis appears continuous across depression of cut. (C) Almost completely restored epidermal thickness, with reduced numbers of pale edematous cells (EC) (H&E, ×300). Inset: transition between normal and pale edematous cells (H&E, ×500).

Discussion

Wound healing in the bottlenose dolphin does not differ dramatically from that reported in terrestrial mammals. Indeed, the sequence of vascular and cellular events corresponds with those reported in rats (Hurley et al. 1966), mice (Croft and Tarin 1970), guinea pigs (Ross and Benditt 1961), rabbits (Matoltsy and Viziam 1970), and man (Ross and Odland 1968).

Healing of cutaneous incisions in dolphins, as in all animals with a vascularized blood system, involves immediate changes in local blood flow which culminate in the infiltration of inflammatory cells into the damaged area. Vascular dilation, congestion, and hemorrhage at 2 h were followed by rounding, or contraction of endothelial cells, extravasation of leukocytes, and edema. Neutrophils predominated inflammatory infiltrates throughout the course of healing. Phagocytosis appears to be a

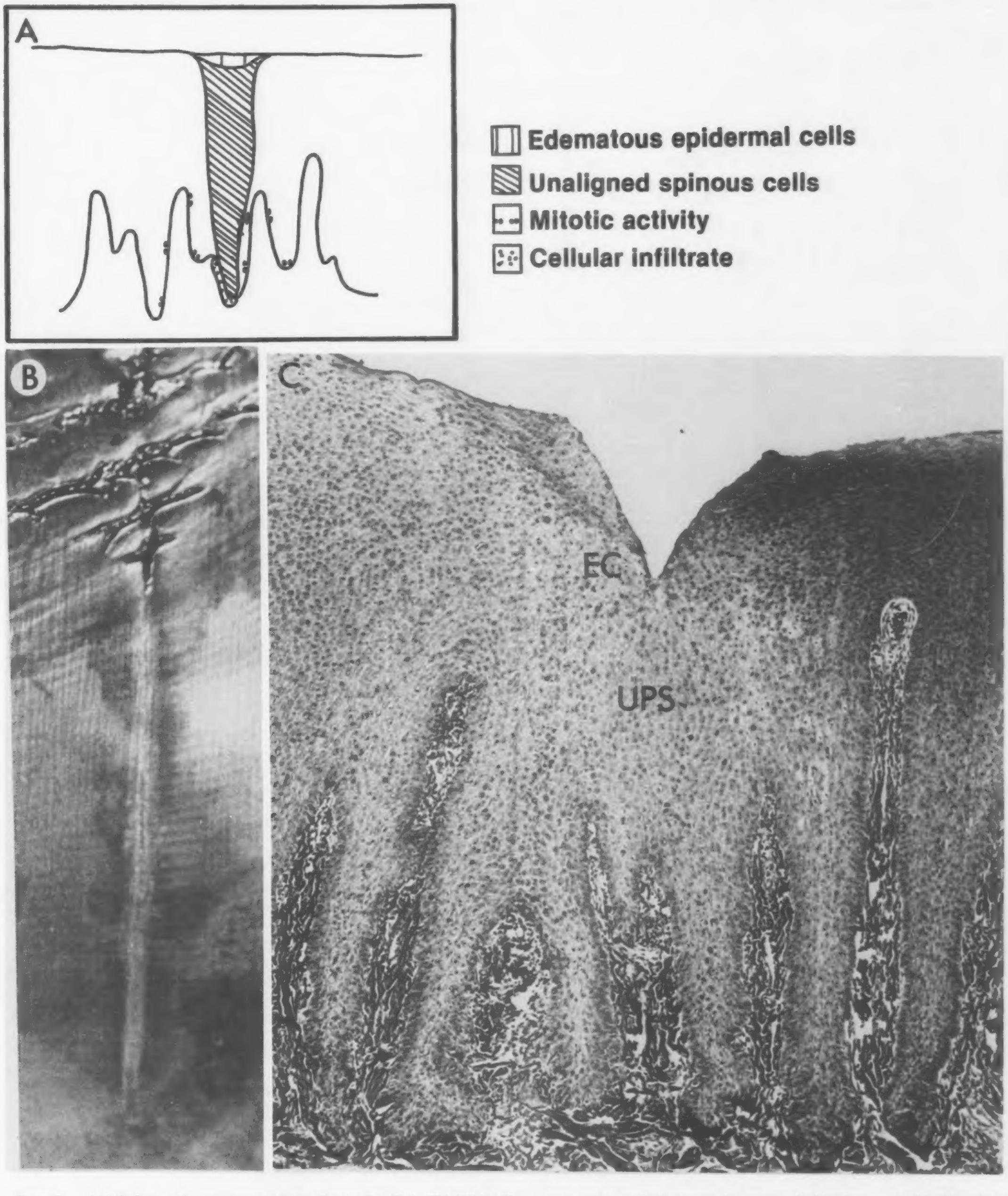

FIG. 7. (A) Schematic representation of cut after 7 d. (B) White linear scar; at top of photograph are parallel "rake marks" inflicted by another dolphin during play behavior. (C) Restored epidermal thickness; a small area of edematous cells (EC) and unaligned, pale spinous cells (UPS) remain beneath the artifactually torn site of incision (H&E, ×171).

key function of these cells in the dolphin, as evidenced by the development of intracellular phagosomes which fuse with cytoplasmic granules, and degranulation of cells with the discharge of contents from the granules. The life span of neutrophils in the wound area was relatively short, only 6–12 h. However, the release of cellular contents and enzymes from necrotic neutrophils early in the response probably continues to contribute to inflammation as it does in other mammals, effecting increased vascular permeability (Juhlin and Hammarstrom 1982), degradation of immune complexes bound on nonphagocytosable surfaces (Henson 1980), and chemotaxis of inflammatory cells (Geotzl and Pickett 1980).

Mononuclear cells appeared in inflammatory infiltrates more frequently subsequent to the peak emigration of neutrophils. This finding supports Ryan's (1967) belief that emigration of inflammatory cells is a biphasic process. The dolphin macro-

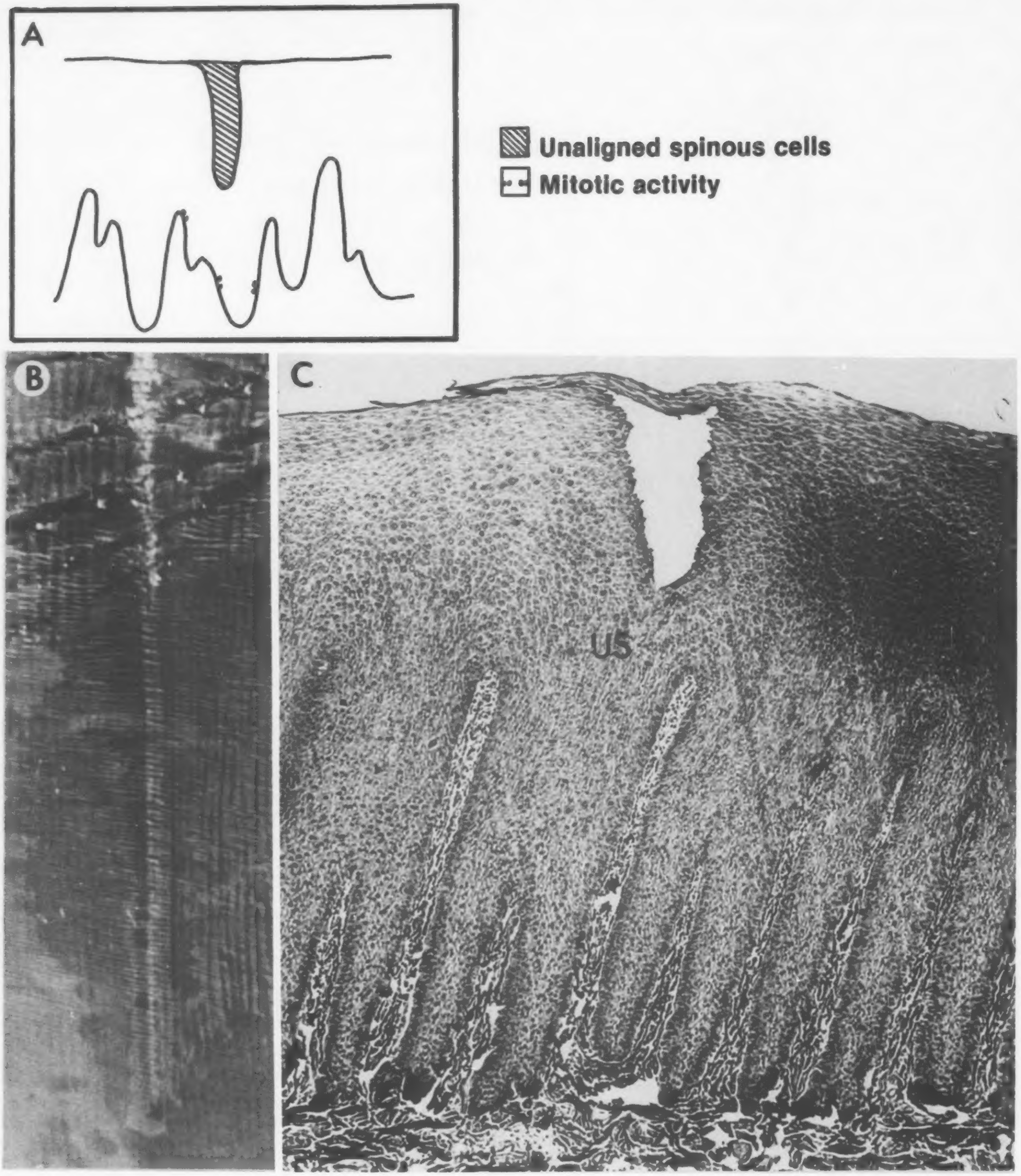

FIG. 8. (A) Schematic representation of cut after 10 d. (B) Linear scar bordered by dark grey band. (C) Site of cut is identified by narrow band of unaligned spinous cells (US) (H&E, ×171). The tear at the incision site, though an artifact of handling, points to the fragility of the repaired skin even after 10 d.

phage is the principal phagocytic inflammatory cell seen to ingest large particles and cellular debris. Lymphocytes were identified infrequently in the cuts and did not share a phagocytic role with macrophages and neutrophils.

Eosinophils were regularly encountered in the cellular infiltrates. Ultrastructurally, cetacean eosinophils differ from those of most terrestrial species in that the granules lack crystalloids. This may signal an evolutionary modification of antigenic properties of the cells (Kay 1979), and it is therefore interesting to note that the lack of a crystalloid is a feature also seen in equine eosinophils. Epidermal cuts in the dolphins were not characterized by a large infiltration of eosinophils, despite high levels in circulation (Medway and Geraci 1978). The phagocytic capabilities of these cells was clearly evident in cellular infiltrates. However, their low occurrence suggests that they do not play an important role in response to mechanical injury.

Concurrent with infiltration of inflammatory cells and wound debridement were changes in the morphology and function of local epidermal cells. The first sign of epidermal involvement in healing was migration of cells using stationary epidermal cells, fibrin, and mesenchymal cells in the dermis as a substrate. Our results support the interpretations of Krawczyk (1971) that epidermal migration is accomplished by the sequential movement of individual cells in a "leap-frog" motion. The retention of few desmosomes between migrating and stationary epidermal cells may permit increased mobility of the cells, while interdigitation of plasma membranes would maintain contact between cells and may provide directional information to the migrating cells.

The elevated mitotic rate of basal epidermal cells is another important epidermal contribution to the reestablishment of normal tissue structure and function. The period of increased mitotic activity in the dolphin is within the range reported for nonoccluded wounds in man (Rovee et al. 1972). Clusters of cells in metaphase were first observed at 48 h, subsequent to the coaption of migrating epidermal cells beneath the cuts. Increased mitotic activity and cellular migration may well have been concurrent processes. However, the peak of mitotic activity was noted only after a continuous germinal layer was established.

Increased mitotic activity is concentrated in the stratum germinativum and overlying few layers within 1 mm of either side of the incisions. The zone of stimulated mitosis is far more restricted than that reported in terrestrial mammals (Silver 1982). To account for the difference, one must consider the microanatomy of normal cetacean skin. The very pronounced dermal papillae provide a large surface area for the stratum germinativum. Consequently, a dolphin has more germinal cells in the immediate area of a given wound, and thus, it seems, can produce the cells required to fill an incisional gap from within a very short distance of the injury.

Though the cuts were histologically repaired by 7 d, they were still grossly visible on the dolphins as white linear marks. The lack of pigment in the repaired incisions was not due to the absence of melanocytes or melanin production, as suggested in terrestrial mammals (Giacometti et al. 1972), but to the diffuse rather than perinuclear distribution of melanosomes within the newly formed spinous cells. Since there was minimal disruption of the melanocyte population by the superficial cuts made in the dolphins, it is expected that normal pigmentation will be restored with time. The possible association between deeper wounds and permanent depigmentation remains for future investigation.

Anderson and Roberts (1975) suggested that rapid wound closure in fish is an important adaptation to an aquatic environment. Likewise, it has been stated that wound healing in cetaceans proceeds at a remarkably fast rate (Greenwood et al. 1974). The present study does not substantiate this claim. Instead, the current findings place the temporal sequence of wound healing in the dolphin within the reported time frame observed for man (Ross and Odland 1968) and rabbits (Matoltsy and Viziam 1970).

The concept of accelerated epidermal healing in dolphins is based primarily on gross observations and extrapolation from histological data of normal cetacean skin. Results of gross observations could be misleading, especially if the observer is unfamiliar with the thickness of the epidermis. That which appears as a deep, serious wound may in fact just enter the superficial dermis. The apparent healing of such a wound within 2 d may be notable in terms of the actual depth of epithelium involved, but relative to the thickness of the epidermis, may be equivalent to the healing of a superficial scrape in a terrestrial mammal. Histological evidence for accelerated epidermal repair is the extensive area of stratum germinativum available for epidermal cell proliferation (Palmer and Weddell 1964), which in combination with a somewhat increased mitotic rate gives a proliferative capacity estimated to be 11.3 times that of man (Brown et al. 1983). Yet the unremarkable rate of reepithelization in the dolphin suggests that wound healing is not the primary function of the large population of proliferative cells in the epidermis.

Though the timing of epidermal repair in *Tursiops* is similar to that in terrestrial mammals, the process is modified owing to intrinsic differences in cetacean skin. A principal distinguishing feature of the healing process in the dolphin was the absence of a scab in the traditional sense of a grossly visible, dry encrustation sealing the wound. Instead, we observed the transformation of exposed surface epidermal layers into degenerating cells intermixed with vesicles. Vesicular changes of this type have been associated with abnormal growth and development of mammalian skin (Ackerman 1978). We do not believe this to be the case in the dolphin. Seawater in contact with epidermal cells causes osmotic shifts and degenerative changes which have been clearly demonstrated in *Tursiops* (Harrison and Thurley 1974). This degenerating layer provides a buffer zone between the environment and the rapidly moving and dividing epidermal cells in the process of closing the wound. The integrity of the buffer layer can be maintained through an equilibrium between continued sloughing, and degeneration of epidermal cells on the opposing side. As the wound closes, this equilibrium shifts toward the regenerative process, leaving only a small focal area of degenerative-vesiculated tissue at the wound opening. In view of the integral role that contact with seawater seems to play in this process, it would be interesting to compare epidermal healing in dolphins in low salinity environments, which they periodically occupy in the wild.

The present study has demonstrated that the inflammatory response and wound healing in the bottlenose dolphin are clearly mammalian in design. However, before simply appending this study to the literature available on terrestrial species, one must consider how the diversity and habitat of cetaceans might influence this basic process. The order Cetacea consists of two distinct suborders, Mysticeti and Odontoceti, and numerous species which range from tropical to polar and from marine to freshwater environments. Moreover, cetaceans in captivity face chlorinated water, unusual diets, and stresses involved with confinement. The present study, done under uniform controlled conditions, can therefore only serve as one step toward our understanding of the inflammatory response and healing in cetacean skin.

Acknowledgements

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Movements of Tagged American Lobsters, *Homarus americanus*, off Southwestern Nova Scotia

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Campbell, A., and A. B. Stasko. 1985. Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 42: 229–238.

A total of 4304 American lobsters (*Homarus americanus*) were tagged and released in inshore areas off southwestern Nova Scotia and on northwest Browns Bank during June–August 1975. Of the 424 lobsters recaptured within 5.4 yr of release, 385 had known recapture locations. For all release areas the average straight-line distance traveled by mature (≥95 mm carapace length) lobsters (15.6 km) was significantly greater than for immature (59–94 mm carapace length) lobsters (4.7 km). Most (69.3%) of the immature lobsters ($N = 212$) were recaptured less than 18.5 km (10 naut mi) from the release sites; for mature lobsters ($N = 173$) this percentage was 40.5%. Previous tagging studies off southwestern Nova Scotia revealed little evidence of long-distance movement; our study, however, shows that mature lobsters can move long distances. Many (19.7%) of the mature lobsters were recaptured more than 92.6 km (50 naut mi) from the release sites. The overall direction of travel was south, in both an east and west direction, with many lobsters moving greater than 50 km from coastal Nova Scotia and Browns Bank into the Gulf of Maine and to the slopes of the continental shelf. Thirteen lobsters moved from Browns Bank to inshore areas of southwestern Nova Scotia. The evidence of the long-distance interchange of a portion of the mature adults between southwestern Nova Scotia and the adjoining continental shelf suggests that lobsters in these areas could belong to a single stock.

De juin à août 1975, un total de 4304 homards d'Amérique (*Homarus americanus*) ont été étiquetés et relâchés dans des zones côtières au large de la côte sud-ouest de la Nouvelle-Écosse et dans la partie nord-ouest du banc Brown. L'endroit de recapture de 385 des 424 animaux repris dans les 5,4 années suivant leur mise en liberté était indiqué. Pour ce qui est de tous les points de lâcher, la distance moyenne en ligne droite (15,6 km) parcourue par les homards matures (longueur de la carapace ≥95 mm) était significativement plus élevée que chez les animaux immatures (4,7 km) (longueur de la carapace = 59–94 mm). La plupart (69,3 %) de ces derniers ($N = 212$) ont été pris à moins de 18,5 km (10 milles marins) du point de lâcher ; chez les homards matures ($N = 173$), cette valeur s'élevait à 40,5 %. Des études d'étiquetage antérieurs menées au large de la côte sud-ouest de la Nouvelle-Écosse n'ont pas révélé de déplacements sur de grandes distances ; par contre, la présente étude prouve que des homards matures peuvent parcourir de grandes distances. Plusieurs (19,7 %) individus matures ont été pris à plus de 92,6 km (50 milles marins) du point de lâcher. En général, ils se dirigeaient vers le sud en voyageant vers l'est ou vers l'ouest ; un grand nombre se sont éloignés de plus de 50 km de la côte de la Nouvelle-Écosse et du banc Brown en direction du golfe du Maine et des pentes de la plate-forme continentale. Treize homards ont migré du banc Brown vers les zones côtières au sud-ouest de la Nouvelle-Écosse. La preuve qu'il existe un échange à longue distance d'une partie de la population d'adultes matures entre le sud-ouest de la Nouvelle-Écosse et la plate-forme continentale adjacente porte à croire que les homards peuplant ces zones appartiennent à un unique stock.

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The coastal waters off southwestern Nova Scotia (Fig. 1) sustain a major American lobster (*Homarus americanus*) fishery (Campbell and Mohn 1983). Fishermen believe that lobsters off southwestern Nova Scotia move from deep to shallow waters in spring and summer (Aiken 1971). This suggestion agrees with observed seasonal shallow-to-deep water movement and mixing of lobsters in the southern New England continental shelf region (Saila and Flowers 1968; Cooper and Uzmann 1971, 1980; Uzmann et al. 1977; Fogarty et al. 1980) and on the continental shelf between Georges Bank and Baccaro Bank (Campbell et al. 1984). However, previous tagging studies off Port Maitland, southwestern Nova Scotia (Wilder and Murray 1958; Campbell 1982), which were of a short-term nature, have provided little insight into long-distance movement of lobsters (Stasko 1980; Campbell 1982).

In 1975, long-lasting sphyrion tags (Scarratt and Elson 1965; Scarratt 1970) were used off southwestern Nova Scotia to determine the extent of lobster movement between inshore and adjacent offshore areas. Stasko and Graham (1976) presented preliminary results from lobsters at liberty less than 8 mo. The present paper provides a detailed analysis of the recaptures up to 1980 and evaluates the long-term movement of immature and mature tagged lobsters off southwestern Nova Scotia.

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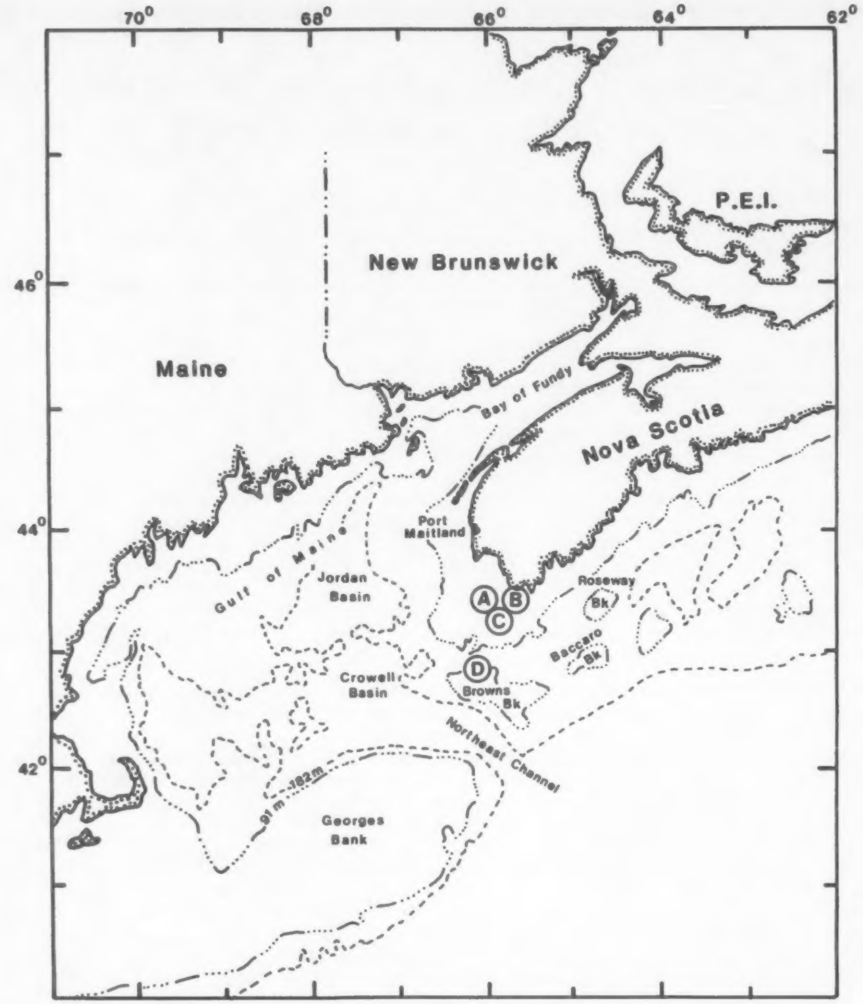

FIG. 1. Tagging sites off southwestern Nova Scotia. A, Seal Island; B, Cape Sable Island; C, Middle Ground; D, northwestern Browns Bank.

Materials and Methods

During June–August 1975, 4304 lobsters (59–158 mm carapace length (CL) measured from the base of the eye socket to the posterior margin of the carapace parallel to the mid-dorsal line) were tagged and released: 57.5% at Seal Island (A), 3.7% at Cape Sable Island (B), 8.8% on Middle Ground (C), and 30.0% on northwestern Browns Bank (D) (Table 1; Fig. 1). These included 44 berried females (104–138 mm CL) caught on Georges Bank and Browns Bank and released off Cape Sable Island (Table 1). The lobsters were caught with baited lobster traps at depths of 4–66 m, and were tagged and released within 30 min of removal from the water and within 2 km of the capture site (with the exception of the 44 displaced berried females which were kept in seawater for about 2 d prior to release). Each lobster was tagged with a sphyrion anchor tag (Scarratt and Elson 1965; Scarratt 1970) with the tag anchor implanted by means of a hypodermic needle into the dorsal musculature between the carapace and abdomen of the lobsters, with the coded yellow tubing protruding dorsally. Release depth, location, date, CL, and sex of each lobster were recorded.

Fishermen were paid a $1 reward for returning a tag with information on recapture date, location, and depth and $3 for allowing a tagged lobster to be measured by Department of Fisheries and Oceans staff. The study was publicized through posters and personal contact with fishermen. Tags were returned through local fisheries officers or directly by mail. As of 31 December 1983, the most recent tag return was on 20 December 1980.

Of the 424 recaptured lobsters (9.9% of total released), data were lacking on recapture locations for 39 and on recapture dates for 14; these could not be used in the relevant analyses. Depth at point of recapture for 32 lobsters was estimated from hydrographic charts. Straight-line distances and direction traveled were determined from the latitude and longitude of release and recapture sites (Campbell et al. 1983). Lobsters were

TABLE 1. Summary release and recapture information for lobsters tagged off southwestern Nova Scotia during 1975. Number of recaptures include individuals with unknown recapture dates and/or locations. Numbers in parentheses denote a group of 44 berried females captured on Georges Bank and Browns Bank and released off Cape Sable Island. Letters in parentheses refer to release locations on Fig. 1, 4, and 5.

	Inshore release areas					
	Seal Island (A)	Cape Sable Island (B)	Middle Ground (C)	Inshore Total	NW Browns Bank (D)	All areas combined
			Release data			
Dates	26 June – 23 July	27 June – 5 August	27 June – 9 July	26 June – 5 August	4 July – 13 August	26 June – 13 August
Mean depth (m)	19.0	28.4 (19.2)	33.5	21.4	39.3	26.8
Mean CL (mm)	87.6	84.8 (115.0)	89.8	88.2	93.5	89.5
Total number released	2474[a]	115 (44)	378	3011	1293[b]	4304
			Recapture data			
Number recaptured	186	8 (6)	26	226	198	424
% recaptured of total releases	7.5	7.0 (13.6)	6.9	7.5	15.3	9.9

[a] Includes 14 berried females (98–120 mm CL) caught in area A.

[b] Includes 26 berried females (95–128 mm CL) caught in area D.

grouped by straight-line distance traveled, i.e. <18.5 km (<10 naut mi), 18.5–36.9 km (10–19 naut mi), 37.0–92.6 km (20–50 naut mi), and >92.6 km (>50 naut mi).

Data of recapture depth and distance traveled were grouped according to season at recapture to investigate the possibility of seasonal movements, (1, January–February–March; 2, April–May–June; 3, July–August–September; 4, October–November–December). Lobsters were categorized by size at release as immature (59–94 mm CL) and mature ($\geqslant 95$ mm CL) based on the median size at physiological maturity (Campbell 1983b; A. Campbell, unpubl. data) estimated with the ovary examination technique (Aiken and Waddy 1980). Mean distance moved, recapture depth, and time at liberty between areas, size groups, and sexes were compared by a one-way ANOVA and the Student–Newman–Keuls test (Kim and Kohout 1975). All comparisons of means were made after $\log_{10}(x + 1)$ transformation of distance moved and $\log_{10} x$ transformation of recapture depth and time at liberty. The geometric means shown are the transformed means of the logarithmically transformed variables.

For each release site and in each size group there were no significant differences ($p > 0.05$) between male and females regarding time at liberty, distance traveled, and recapture depth; consequently, both sexes (including berried females) were combined for each size group and area. Data on movements for all three inshore areas were combined, since there were no significant differences ($p > 0.05$) in distance moved, depth at recapture, and time at liberty among the three areas.

The following equations on the direction of movement were computed according to Jones (1959) and Saila and Flowers (1968), using a computer program developed by Campbell et al. (1983).

North–south direction component (km/d):

$$(1) \quad V = \frac{\Sigma\, r \cos \theta}{\Sigma\, t}$$

East–west direction component (km/d):

$$(2) \quad V' = \frac{\Sigma\, r \sin \theta}{\Sigma\, t}$$

Mean vector angle:

$$(3) \quad \bar{\theta} = \text{arc tan} \frac{\Sigma\, r \sin \theta}{\Sigma\, r \cos \theta}$$

Rayleigh test:

$$(4) \quad Z = R^2/n$$

where n = number of individual tag returns,

$$R = \sqrt{(\Sigma \sin \theta)^2 + (\Sigma \cos \theta)^2},$$

r = apparent "straight-line" distance traveled (km) from release to recapture point, θ = angle of direction of travel based on deviation from true north, and t = time (d) from release to recapture.

Results

Time at Liberty

Of the lobsters released inshore, 7.5% were recaptured, and of those released offshore, 15.3% were recaptured (Table 1). Most lobsters were recaptured within a year of release; the percentage returns generally decreased with increased time at liberty (Fig. 2). The mean time between release and recapture was significantly longer ($p < 0.01$) for Browns Bank releases than for inshore releases (Fig. 2).

Distance Moved

In both release areas combined, mature lobsters (15.6 km) moved a greater mean distance ($p < 0.01$) than immature lobsters (4.7 km). The majority (69.3%) of recaptured lobsters that were immature at release had moved less than 18.5 km from all the release sites; only a few (8.0%) moved more than 92.6 km. By contrast, less than half (40.5%) of the lobsters that were mature at release were caught less than 18.5 km, and 19.7% were caught more than 92.6 km from all the release sites. There was no significant difference ($p > 0.05$) in the mean distance moved by mature lobsters from the inshore and Browns Bank release areas (Table 2). However, immature lobsters

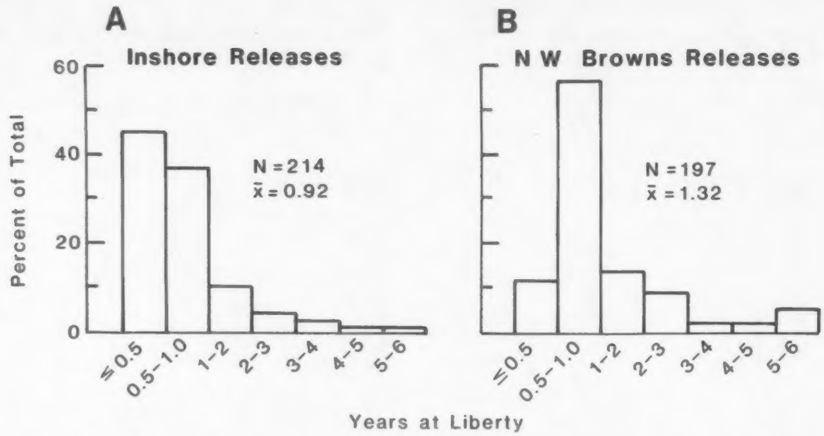

FIG. 2. Percentage of tag returns as a function of time at liberty for lobsters released (A) in inshore areas off southwestern Nova Scotia and (B) on northwestern Browns Bank, summer 1975; $\bar{x}$ = arithmetic mean; N = number of individuals.

TABLE 2. Percentage of total recaptures and mean distance moved of lobsters tagged in the inshore area of southwestern Nova Scotia and on northwestern Browns Bank. Immature lobsters are 59–94 mm CL and mature lobsters ≥95 mm CL at release. Equality of means tested by ANOVA after $\log_{10}(x + 1)$ transformation of data, $F_{(3,381)} = 17.05$, $p < 0.01$; means sharing the same letter in the same row are not significantly different ($p > 0.05$); means not sharing same letter are significantly different ($p < 0.01$) by the Student–Newman–Keuls test.

	Inshore areas		NW Browns Bank	
	Immature	Mature	Immature	Mature
% of total recaptures that moved (km)				
<18.5	66.7	49.3	73.0	33.3
18.5–36.9	22.8	27.3	3.4	15.6
37.0–92.6	1.6	3.9	16.8	31.3
>92.6	8.9	19.5	6.8	19.8
Mean (arithmetic) km moved	22.6	36.1	22.3	46.2
Mean (geometric) km moved	7.3 a	15.3 b	2.4 c	15.8 b
Maximum km moved	239.8	145.1	200.0	155.5
Total recaptures				
Distance (known)	123	77	89	96
Distance (unknown)	(15)	(11)	(7)	(6)

released in the inshore areas moved a significantly greater mean distance ($p < 0.01$) than those from Browns Bank (Table 2).

There was a general trend for lobsters, especially immature lobsters, with increasing time at liberty to be caught further from the release location although a few were still caught close to the release site even after more than a year (Fig. 3). The longest straight-line movement (239.8 km) recorded in this study was for an immature female (81 mm CL) after 3.0 yr at liberty by which time she had grown to maturity (112 mm CL).

Directional Movement

The straight-line tracks between release and recapture points indicate exchange between inshore and offshore areas off southwestern Nova Scotia (Fig. 4–7). Eight lobsters crossed the northwestern channel between Browns Bank and Georges Bank (Fig. 5, 7). Many lobsters from both the inshore areas and Browns Bank were recaptured near the edge of the continental shelf and in Crowell Basin and Truxton Swell (Fig. 5, 7). Thirteen lobsters from northwestern Browns Bank were recaptured inshore (Fig. 7). Of the 44 berried females displaced from offshore areas and released off Cape Sable Island, 6 were recaptured 0.35–0.85 yr later; 2 were captured less than 10 km from their release point and 4 were recaptured on the edge of the continental shelf south of Browns Bank (Fig. 5). One displaced berried female moved 128.8 km to the continental slope within 0.35 yr of release. These distances traveled were not significantly different ($p > 0.05$) from those of other mature lobsters (including berried females) caught and released inshore.

The directional movement of most returns was south and east for immature and mature lobsters (Table 3). The mean vector angles ($\bar{\theta}$) ranged from 138.9 to 177.1° from true north, with the Rayleigh tests indicating a nonuniform distribution for most areas when all recaptures were combined. In general, the

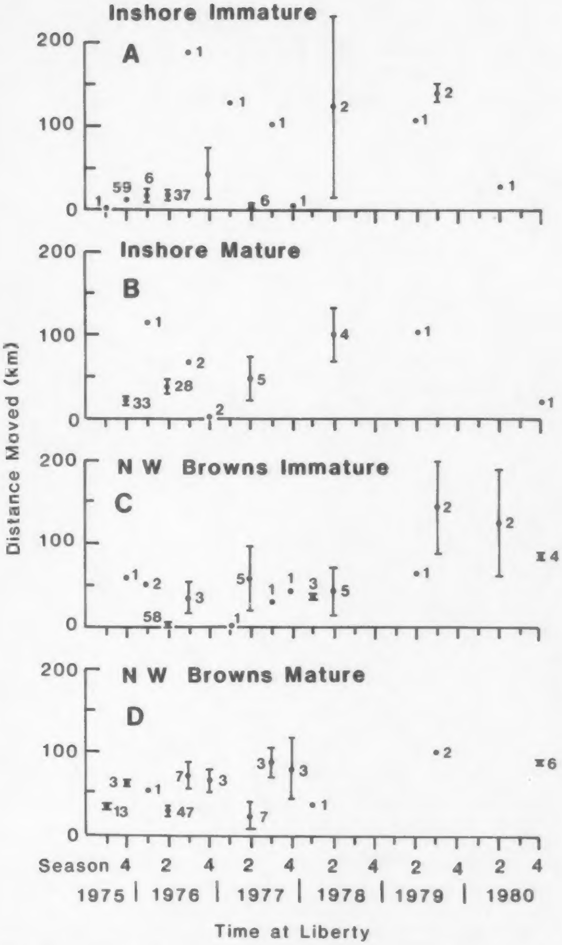

FIG. 3. Mean straight-line distance moved (km) grouped by seasonal (quarterly) periods of tagged (A) immature and (B) mature lobsters released inshore southwestern Nova Scotia and for (C) immature and (D) mature lobsters released on Browns Bank. Dots = arithmetic means; vertical lines = ±1 SE; number at each dot = number of individuals recaptured.

north–south were stronger than the east–west vector components. The negative north–south vector components (i.e. southerly movement) were undoubtedly influenced by the constraints imposed by the coastline of Nova Scotia. Estimates of V and V' reflect, in part, the distances traveled, whereas the Rayleigh test is mainly influenced by the direction of travel. The Rayleigh test gives equal weight to each tag return; consequently, any detectable movement in any direction would influence the direction analyses.

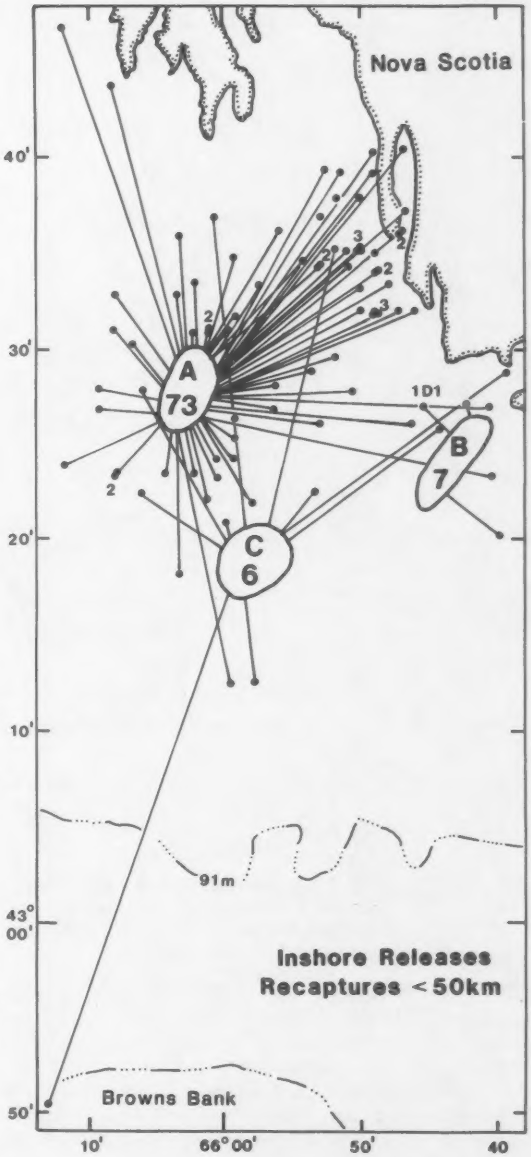

FIG. 4. Release and recapture points with straight-line distances moved <50 km for tagged lobsters released at (A) Seal Island, (B) Cape Sable Island, and (C) Middle Ground off southwestern Nova Scotia. Each dot represents one recapture unless otherwise indicated. Dot with 1D1 indicates two lobsters caught at same location including one of the displaced berried females (see text for explanation). Numbers in large irregular circles indicate number of recaptures within 15 km from release sites.

Analysis for the possibility of directed seasonal movements by partitioning time-at-liberty data into seasonal periods was hampered by having only seasonal periods with sufficient returns ($n \geq 2$) limited to the first year (Table 3). Immature and mature lobsters released in the inshore areas and recaptured during season 4 in 1975 and season 1 in 1976 showed northerly and easterly shoreward movement (Fig. 4), and the Rayleigh tests indicated, in general, a nonuniform distribution of returns (Table 3). This movement may partly reflect the intense fishing effort in the inshore areas, mostly to the north of the release sites, during the November–December fishing season. However, during the next spring fishing period there was a significant shift of recaptures to the southeast direction for the immature lobsters released in the inshore areas, although the distances traveled were not as great as for the mature lobsters (Table 3). The southwest direction of the mean vector angle

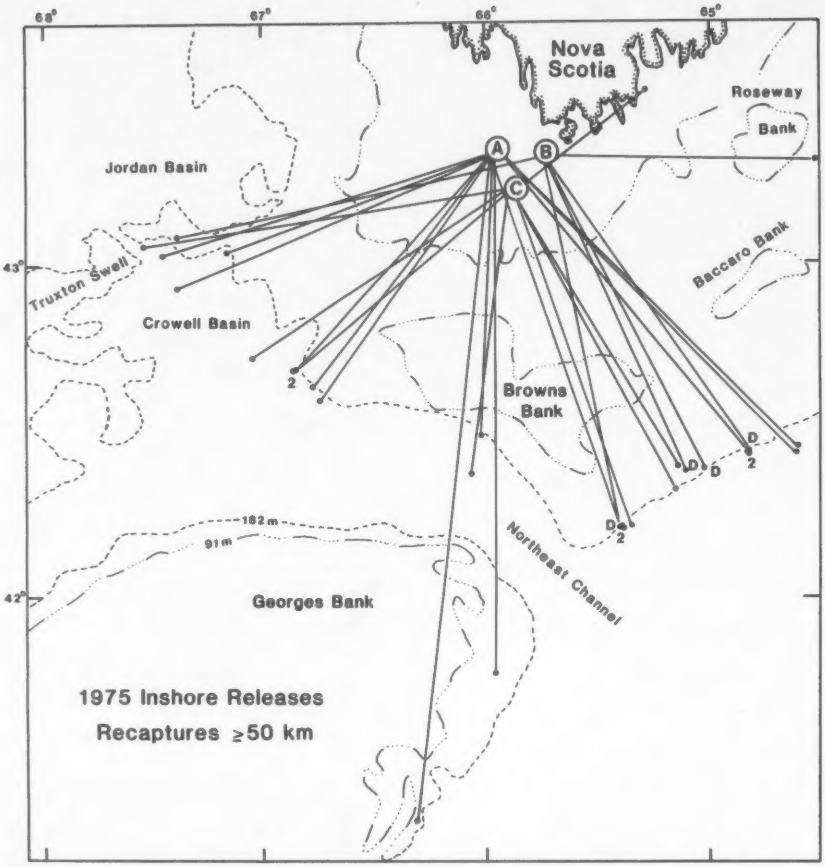

FIG. 5. Release and recapture points with straight-line distances moved ≥50 km for tagged lobsters released at (A) Seal Island, (B) Cape Sable Island, and (C) Middle Ground off southwestern Nova Scotia. Each dot represents one recapture unless otherwise indicated. The letter "D" at a dot indicates recapture of a displaced berried female.

(192.5°) was not significant ($p > 0.05$) for "inshore" mature lobsters recaptured during season 2 of 1976, indicating that their long distance movement was not in a uniform direction (Table 3; Fig. 5). For lobsters released on Browns Bank the variability in directional movement in each season is difficult to interpret. Generally, lobsters from Browns Bank had moved south with some westerly or easterly directional component, depending on the season examined (Table 3).

Recapture Depth

Mean depths at recapture were significantly greater ($F_{3,388} = 60.3$, $p < 0.01$) for mature (geometric mean = 26.9 m) than for immature lobsters (19.1 m) released at inshore areas, and for mature (86.4 m) compared with immature lobsters (52.4 m) released on Browns Bank. Examination of depths at recapture by season did not show any recognizable pattern. The number of recaptures was small for such detailed analysis and the uneven seasonal fishing effort makes interpretation difficult.

Discussion

In contrast with previous studies off southwestern Nova Scotia, which revealed little evidence of long-distance movement (Wilder and Murray 1958; Campbell 1982), our study demonstrates that some mature male and female American lobsters move long distances and that mature lobsters move greater distances than immature lobsters. Previous studies in the area were designed primarily to estimate exploitation rates mainly for immature lobsters released prior to the fishing season and utilized carapace tags that were lost at molt. In the present study a long-term tag was used, which is not lost at molt, and the tagged lobsters were released during the summer when the inshore lobster fishing season was closed. Thus, the tagged lobsters had several months to disperse before the start of the fishing season.

Previous lobster tagging studies conducted in coastal waters of eastern North America indicate localized lobster movements (Templeman 1935, 1940; Wilder 1963; Cooper 1970; Stewart 1972; Cooper et al. 1975; Fogarty et al. 1980; Krouse 1980, 1981; Stasko 1980; Ennis 1984). Few lobsters tagged at inshore locations have traveled considerable distances (Morrissey 1971; Dow 1974; Fogarty et al. 1980; Krouse 1981; Campbell 1984). Some long-distance movements (>100 km) have been recorded for lobsters tagged and released in waters off New England and on the continental shelf (Saila and Flowers 1968; Cooper and Uzmann 1971; Uzmann et al. 1977; Fogarty et al.

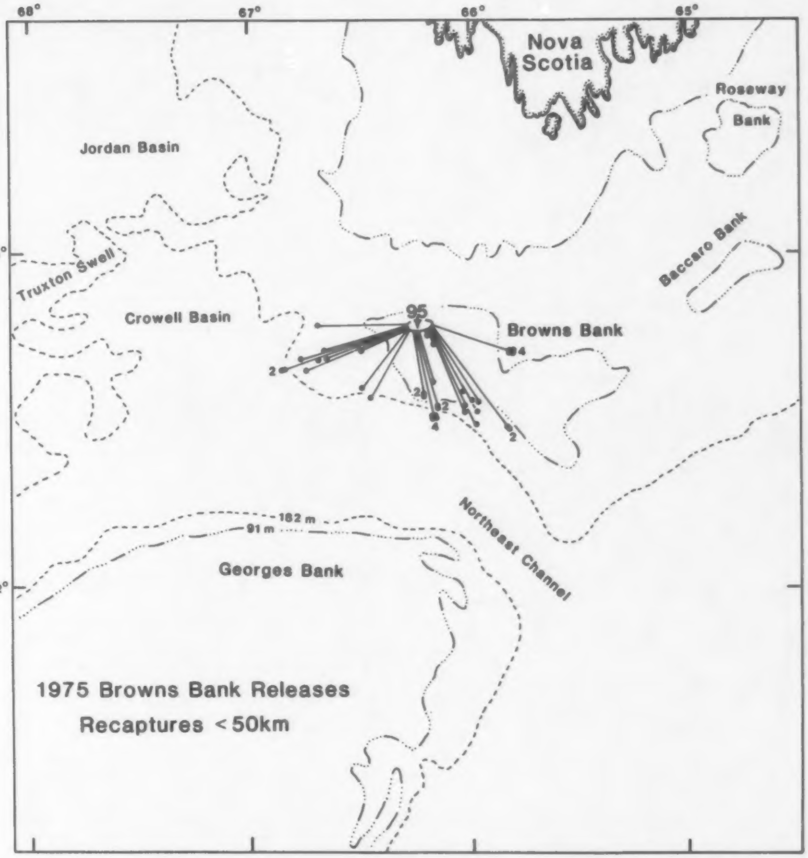

FIG. 6. Release and recapture points with straight-line distances moved <50 km for tagged lobsters released on northwestern Browns Bank. Each dot represents one recapture unless otherwise indicated. Number in oval indicates number of recaptures within 15 km from release sites.

1980) and the continental shelf closer to southwestern Nova Scotia (Campbell et al. 1984).

Our study is the first to demonstrate empirically that mature lobsters move greater distances than immature lobsters in both inshore and offshore areas of southwestern Nova Scotia. There is no clear indication from the data to explain why mature lobsters moved further than immature lobsters. Mature lobsters may have moved seasonally to different depths to obtain sufficiently high temperature to optimize their physiological requirements of molting and egg extrusion (Cooper and Uzmann 1971, 1980). In our study some lobsters that were immature at release grew to mature sizes during their time at liberty; this would account for some individuals moving greater distances than most immature lobsters. Of the 17 immature lobsters at release that moved more than 92.6 km, the average time between release and recapture was 2.5 yr, spanning two to three molt periods. The molting period off southwestern Nova Scotia is June–November (Wilder 1953; Campbell 1983a, 1983b).

The effectiveness of our tag return system is difficult to assess, and undoubtedly some recaptured lobsters were not reported. Stasko and Graham (1976) found that cooperation from fishermen in returning tags was excellent until early January 1976. There is some doubt about the completeness of reporting after that, since there was considerable conflict between inshore and offshore lobster fishermen over the perceived management implications emanating from the results of this study. However, many tags were returned in the spring of 1976 from both the inshore and offshore areas (Fig. 2, 3). Indeed, most lobster fishermen contacted by fisheries personnel continued to provide information on tag returns throughout the 5.4-yr study. The percentage of tags returned in this study (9.9%) is comparable with the returns (13.5%) of tagged lobsters released off Port Maitland in June 1979, although not as high as the returns (mean 50%) of tags released just prior to the opening of the fishing season (late November) off Port Maitland during 1949–80 (Campbell 1982). The low return rate for the inshore area was probably due to the summer-released lobsters having (1) a chance to disperse during several months of the closed fishing season, (2) a high mortality during the molt period, or (3) some tag returns not being reported.

Mixing of mature lobsters among inshore southwestern Nova Scotia, Browns Bank, and other offshore areas is evident from this study. The extent of this mixing is difficult to determine and interpretation of the movement data should be made with caution. The simple estimation of straight-line distances from single recapture (as opposed to multiple recapture) data seldom

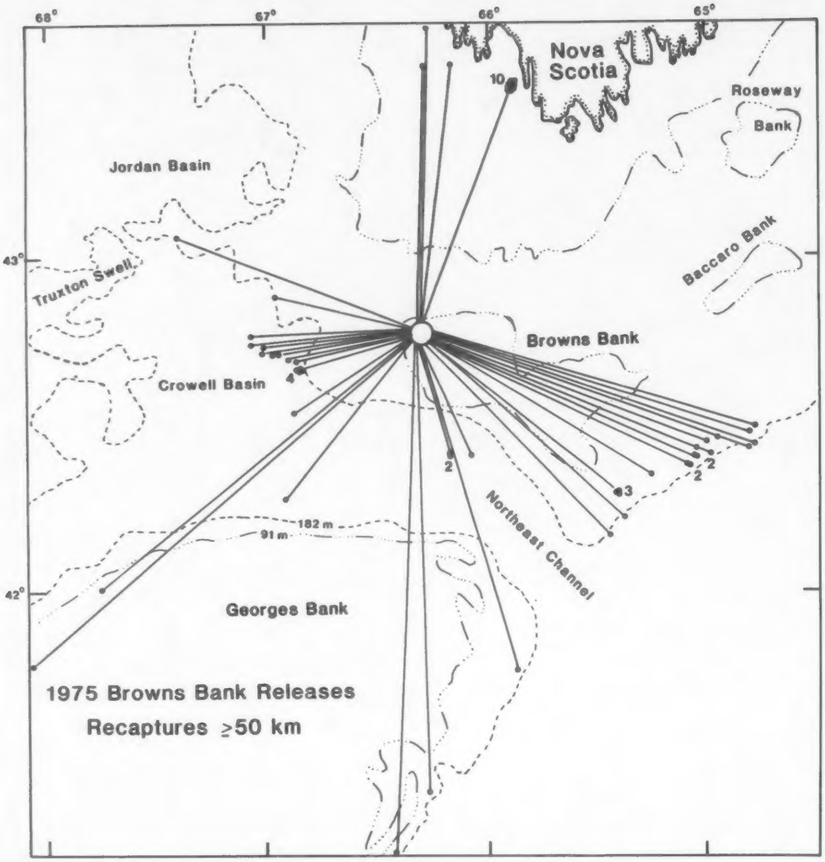

FIG. 7. Release and recapture points with straight-line distances moved ≥50 km for tagged lobsters released on northwestern Browns Bank. Each dot represents one recapture unless otherwise indicated.

provides an accurate picture of lobster movements. However simplistic, the straight-line movement data do provide a general overview of long-term dispersal of lobsters. Bias may be introduced, however, by the nonuniform distribution of fishing effort both in time and space. In the offshore waters, although there is no closed season, fishing effort is reduced in the winter months; most offshore lobsters are caught during May, June, and July (Pezzack and Duggan 1983). The inshore fishery off southwestern Nova Scotia is open from the last Tuesday in November to the end of May. In practice, the main fishing effort occurs in late November – December and in April–May, with much reduced fishing during January–March. The uneven temporal fishing effort may explain the uneven seasonal distribution of tag returns, especially in the first year at liberty (Fig. 2, 3). In our study, the lack of fishing in certain seasons would mask any seasonal movements of lobsters between deep and shallow waters, such as have been demonstrated in other areas (Montreuil 1953, 1954; Bergeron 1967; Cooper and Uzmann 1971; Uzmann et al. 1977; Fogarty et al. 1980; Munro and Therriault 1983; Campbell et al. 1984; Ennis 1984).

Nonuniform spatial patterns of fishing effort may introduce an apparent directional component in what might otherwise be random movement. Few lobsters were caught in the middle grounds between inshore southwestern Nova Scotia and Browns Bank and on the eastern shallow areas of Browns Bank. This is partly a reflection of the fishing effort which is concentrated in the inshore areas and along the edge of the continental shelf (Stasko and Campbell 1980; Stasko and Pye 1980; Pezzack 1983; Pezzack and Duggan 1983). Although commercial lobster fishermen concentrate their fishing effort in areas of high productivity where lobster densities are highest, they regularly place exploratory traps in areas that are considered marginally profitable. Consequently, fishing effort distribution should reflect the location of lobster concentrations. The closure of a large area of Browns Bank to lobster fishing since 1979 (Pezzack and Duggan 1983) should not affect the general conclusions of this study, as most tags were returned prior to 1979.

Although immature lobsters seem to have low dispersal tendencies, the long-distance movement of mature lobsters suggests that some intermixing of lobsters occurs between inshore and offshore areas in the Gulf of Maine and the adjoining continental shelf. Our findings support the hypothesis that there is a single stock of lobsters in the northern Gulf of Maine and adjoining continental shelf (see Campbell and Mohn 1983 for a review). The single stock concept has important implications, since the heavily fished coastal areas (Campbell 1980) may be dependent on larval recruitment from outside areas. Indeed the source of larval recruitment in southwestern

TABLE 3. Direction statistics for tagged immature (<95 mm CL) and mature (≥95 mm CL) lobsters released in the inshore areas of southwestern Nova Scotia and on northwestern Browns Bank. $\bar{\theta}$ = mean vector angle from true north; V and V' = nonrandom directed movement along the north–south and east–west plane, respectively; negative values of V and V' indicate net southerly and westerly movement, respectively; R and Z = Rayleigh test statistics for randomness of distribution of points about a circle; N = number of individuals; * = significant at $p < 0.01$ indicating a nonuniform distribution (Batschalet 1965); both sexes are combined; only the first four seasons shown when $N \geqslant 2$; total includes recaptures for all years that have known dates and locations of recapture.

Maturity	Year	Season	$\bar{\theta}$	V (km/d)	V' (km/d)	R	Z	N
			Inshore area					
Immature	1975	4	32.6	0.035	0.023	19.43	6.40*	59
	1976	1	8.0	0.034	0.005	2.18	0.79	6
		2	113.5	−0.009	0.022	19.29	10.05*	37
	1975–80	Total	139.9	−0.013	0.011	40.06	13.05*	123
Mature	1975	4	61.7	0.020	0.038	18.51	10.38*	33
	1976	2	192.5	−0.056	−0.012	5.33	1.01	28
	1975–80	Total	167.9	−0.039	0.008	22.88	6.80*	77
			NW Browns Bank					
Immature	1976	1	251.3	−0.083	−0.247	1.99	1.99	2
		2	127.6	−0.001	0.002	50.34	43.70*	58
	1975–80	Total	177.1	−0.014	0.001	49.18	27.17*	89
Mature	1975	3	196.8	−0.785	−0.238	9.80	7.39*	13
		4	258.4	−0.139	−0.675	3.00	3.00	3
	1976	2	131.1	−0.024	0.028	19.45	8.05*	47
	1975–80	Total	148.2	−0.027	0.017	6.79	0.48	96

Nova Scotia is unknown and may be based partially on long-distance larval drift from Browns and Georges Banks (Stasko 1978; Stasko and Campbell 1980; Harding et al. 1983; Stasko and Gordon 1983) and/or may be a local phenomenon in some areas, closely related to local availability of berried females hatching eggs. The relationship between the seasonal movements of adult lobsters, larval recruitment patterns, and oceanographic features is, however, still unclear.

Acknowledgments

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Modelling Winter Oxygen Depletion Rates in Ice-Covered Temperate Zone Lakes in Canada

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Babin, J., and E. E. Prepas. 1985. Modelling winter oxygen depletion rates in ice-covered temperate zone lakes in Canada. Can. J. Fish. Aquat. Sci. 42: 239–249.

Winter oxygen depletion rates (WODR) ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$) were determined for 13 lakes in central Alberta during the winter of 1982–83. Although dissolved oxygen decreased in all lakes for the first 3.5 mo after freeze-up, the decreases were nonlinear. The highest WODR were observed just after freeze-up. The nonlinear WODR were significantly correlated with two estimates of lake productivity (i.e. total phosphorus and chlorophyll *a*, $P < 0.05$) but were not significantly correlated with morphometry (e.g. mean depth). When the WODR from the Albertan lakes were treated as linear, to enable a comparison with other studies, correlations were found between WODR and morphometry, and WODR and estimates of summer productivity. These relationships were significantly different from observations by previous investigators who worked on ice-covered lakes in two other regions. When data from other ice-covered lakes were combined with this study, WODR were best predicted from a combination of mean summer TP (TP_{su} in $mg \cdot m^{-2}$) in the euphotic zone and mean depth ($\bar{z}$ in m):

$$\text{WODR} = -0.101 + 0.00247\text{TP}_{su} + 0.0134\bar{z} \qquad r = 0.90.$$

The above equation permits the prediction of WODR for a greater range of lake types than previous models.

Les taux d'appauvrissement hivernal en oxygène (TAHO) ($g\ O_2 \cdot m^{-2} \cdot jour^{-1}$) ont été quantifiées dans 13 lacs du centre de l'Alberta pendant l'hiver de 1982–83. La concentration d'oxygène dissous a baissé pendant les premiers 3,5 mo après le gel dans tous les lacs, mais ces diminutions n'étaient pas linéaires. Le taux le plus élevé a été observé juste après le gel. Les TAHO non linéaires étaient en corrélation significative avec deux estimations de la productivité lacustre (c.-à-d. le phosphore total et le chlorophylle *a*, $P < 0,05$) mais non avec la morphométrie (par ex. la profondeur moyenne). Une comparaison des TAHO des lacs albertains, considérés linéaires, avec ceux tirés d'autres études a révélé des corrélations entre les TAHO et la morphométrie et les TAHO et la productivité estivale. Ces relations étaient significativement différentes des observations effectuées par d'autres chercheurs qui ont étudié des lacs gelés de deux autres régions. On a obtenu une meilleure prédiction des TAHO en combinant la productivité moyenne totale en été ($PT_{été}$ en $mg \cdot m^{-2}$) dans la zone euphotique et la profondeur moyenne ($\bar{z}$ en m), à l'aide des données de l'étude et des données recueillies dans d'autres lacs gelés. L'équation ainsi obtenue :

$$\text{TAHO} = -0{,}101 + 0{,}00247\text{PT}_{été} + 0{,}0134\bar{z} \qquad r = 0{,}90$$

permet la prédiction du TAHO dans une plus grande variété de lacs que les modèles précédents.

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Several investigators have examined patterns in winter oxygen depletion rates (WODR) (Welch et al. 1976; Barica and Mathias 1979), factors controlling WODR (e.g. Mathias and Barica 1980), and ways to reduce WODR (Wirth 1970; Barica et al. 1983). Recently, Jackson and Lasenby (1982) constructed two models to predict oxygen profiles under ice in lakes located on the Precambrian Shield and in limestone basins in Ontario.

Winter oxygen depletion rates have been studied in two extreme lake types in temperate regions of Canada: the relatively deep, oligotrophic lakes on the Precambrian Shield (Welch et al. 1976) and the shallow, eutrophic, prairie pothole lakes in southwestern Manitoba (Barica and Mathias 1979) (mean depths ($\bar{z}$) ranged from 4 to 27 and 2 to 4 m and mean summer chlorophyll *a* (Chl *a*) concentrations in the euphotic zone ranged from 1 to 2 and 5 to 102 $mg \cdot m^{-3}$, respectively, for the two lake types). Although $\bar{z}$ was the best predictor of WODR in both lake types, the mathematical relationships were different (Welch et al. 1976; Barica and Mathias 1979). Thus, empirical models to predict WODR pertain to relatively specific lake types in certain geographic regions.

Winter oxygen depletion rates may also be affected by the amount of organic material produced in a lake (Mathias and Barica 1980) and thickness of the snow cover (Barica et al. 1983). However, the effects of lake productivity and/or snow cover on WODR have never been quantified. In contrast, models to predict summer areal hypolimnetic oxygen deficits (AHOD) do incorporate measures of hypolimnetic morphometry and lake productivity (Cornett and Rigler 1979, 1980; Charlton 1980).

Winterkill is a common phenomenon in lakes in central Alberta. Thus, considerable interest exists in factors controlling WODR in these lakes. However, Albertan lakes are different from other temperate zone lakes studied in Canada; they may be as productive as the prairie pothole lakes, but are much deeper (Prepas and Trew 1983). We collected data on 13 lakes to test whether either existing WODR model is applicable to Albertan lakes. These data were also used to construct an empirical model to predict WODR for Albertan lakes, and were combined with other data in the literature to test the contribution of lake productivity to WODR. Furthermore, we used data collected from the Albertan lakes to test the models to predict oxygen profiles under ice-cover. The latter were developed with data from lakes on the Precambrian Shield and in limestone basins in Ontario (Jackson and Lasenby 1982).

To estimate WODR, water samples are collected over the deepest part and treated as representative of the whole lake (Welch et al. 1976; Barica and Mathias 1979; Jackson and Lasenby 1982). This approach assumes that oxygen concentrations are homogeneous within horizontal strata, an hypothesis that has never been rigorously tested. To determine if one-site-sampling is adequate for estimating whole-lake oxygen mass, samples were collected from six to seven sites in each of five lakes for comparison with results from a single station.

Summer AHOD models incorporate estimates of open-water productivity and lake morphometry (Cornett and Rigler 1979, 1980; Charlton 1980). Since an ice-covered lake is analogous to the hypolimnion of a stratified lake in the summer, we tested the ability of four AHOD models to predict WODR in the Albertan lakes.

Study Lakes

The 13 lakes in this study are located in central Alberta within a 160-km radius of the city of Edmonton. The lakes range in size from 0.08 to 4.4 km^2. All lakes are underlain by 10–40 m of glacial till. Total dissolved solids in the lakes ranges from 150 to 390 $mg \cdot L^{-1}$ and color ranges from 2 to 25 mg $platinum \cdot L^{-1}$. The lakes were chosen to encompass large ranges in morphometry and productivity: $\bar{z}$ of the lakes ranges from 3 to 19 m and trophic status varies from oligotrophic to hypereutrophic (mean summer euphotic zone Chl *a* ranges from 2 to 155 $mg \cdot m^{-3}$). Background data for the lakes are in Prepas and Trew (1983) and E. E. Prepas and I. C. Wisheu (unpubl. data). Two lakes, Amisk and Baptiste, have distinct north and south basins. Both basins of Amisk were sampled as was the deep south basin of Baptiste; all three basins were treated as separate lakes. Each of the remaining lakes was sampled at only one site. Seven of these lakes have simple basins with a single deep spot; two lakes, Eden and Sauer, each have two distinct deep spots; and the remaining lake, Hubbles, has three deep spots. None of the study lakes has major surface inflows or outflows; hence, the main source of organic matter in the lakes is from autochthonous production.

Materials and Methods

The study lakes were permanently ice-covered by November 5–11, 1982, and remained frozen until the 3rd wk in April 1983. Each lake was visited 7–13 times from just prior to freeze-up until 1 mo before break-up. On each visit, water samples were collected over the deepest part of the lake with an aluminum drop-sleeve water bottle. Water for dissolved oxygen (DO) analyses was collected every 1 or 2 m from the top of the hydrostatic water level to the lake bottom or to where it became anoxic as evidenced by the smell of hydrogen sulfide. These samples were fixed immediately (Carpenter 1965) and, to avoid freezing, transported back to the laboratory in insulated boxes containing hot-water bottles.

To determine the potential contribution of algae to the lake oxygen mass under ice-cover, we collected water for Chl *a* analyses. For the first 1.5 mo, samples were collected at 1-m intervals from 1 to 4 m below the hydrostatic water level, and for the remainder of the winter, samples were collected to a depth of 5–24 m and pooled into strata 2–6 m deep. Water samples for Chl *a* analyses were placed in 2-L amber Nalgene bottles and transported to the laboratory. To estimate spring and summer productivity in the lakes, we took total phosphorus (TP) and Chl *a* levels in the euphotic zone for 10 of the lakes from Prepas and Vickery (1984). For two lakes, Nakamun and Halfmoon, TP and Chl *a* values are from Riley (1983). The 13th lake, Hubbles, was sampled five times from May 14 to August 26, 1982. In this study, water samples for TP and Chl *a* analyses were collected with Tygon tubing at three stations and pooled. These samples were collected from the euphotic zone, defined as the depth to 1% surface irradiance as measured with a Lambda LI-185 light meter equipped with an underwater sensor, or 2 times Secchi disc depth (SD).

To determine whether organic content of the sediments is correlated with WODR, we took sediment samples from 12 of the study lakes during the summers of 1982 and 1983. The number of samples collected (four to eight) on each lake increased in proportion to lake size. These samples were collected randomly from each lake with a four-barrel corer (Hamilton et al. 1970). The top 5 cm was removed from each core and pooled with other cores from that site. Due to the flocculent nature of the sediments, we arbitrarily chose the top 5 cm for the determination of organic content. Also, results from another study on a central Albertan lake showed that the sediments were totally mixed to a depth of 8 cm (Reynoldson and Hamilton 1982). The samples were brought back to the laboratory and frozen until they could be analyzed for loss on ignition (LOI).

Detailed morphometric data were already available for five of the study lakes (E. E. Prepas and D. O. Trew, unpubl. data). The remaining eight lakes were sounded with a Furuno model FE-400 depth sounder. Morphometric data were determined from the bathymetric maps with a Tallos digitizer connected to a Hewlett-Packard 9825B desk-top computer supplied by Alberta Energy and Natural Resources.

Dissolved oxygen concentration was determined on duplicate water samples based on Carpenter's (1965) modification of the Winkler technique. Most samples were titrated within 12 h of collection and all were titrated within 24 h. To determine the accuracy of the method for collecting DO samples, the average DO values from duplicate water samples were compared. The average difference between independent oxygen samples collected at the same site and depth was 0.07 $mg \cdot L^{-1}$ and the range was 0.01–0.32 $mg \cdot L^{-1}$. Percent oxygen saturation of the lakes was determined based on oxygen saturation tables in Cole (1983). Duplicate samples for Chl *a* analyses were prepared within 12 h of collection by filtering 0.05–2 L of lake water, depending on cell density, through glass fiber filters. Chlorophyll *a* was determined with the ethanol extraction technique of Bergmann and Peters (1980). Total phosphorus was determined on duplicate 50-mL samples of lake water with the persulfate method of Prepas and Rigler (1982). Loss on ignition was determined by the weight loss of dried sediment samples baked at 550°C for 24 h. The LOI was not corrected for dehydration of the samples (Hargrave 1975). Loss on ignition estimates for all samples on each lake were combined to yield an average whole-lake estimate.

For each winter visit, oxygen mass was determined for each stratum from the product of stratum volume and oxygen concentration; these data were summed to yield whole-lake oxygen mass. The volume of the top 1 m was corrected for ice thickness. The whole-lake oxygen mass was divided by the under-ice surface area of the lake to yield the areal oxygen mass ($gO_2 \cdot m^{-2}$) (Welch 1974). To calculate WODR ($gO_2 \cdot m^{-2} \cdot d^{-1}$), areal oxygen mass was regressed against days past freeze-up; the slope of this regression line is the WODR.

To develope empirical models for the lakes in central Alberta, WODR were regressed against estimates of spring and summer productivity (TP, Chl *a* and LOI) and mean and maximum depth ($\bar{z}$ and Z_{max}, respectively). For the Alberta lakes, spring was defined as May 27 – June 14 and summer was defined as June 15 – September 15 (after Prepas and Vickery 1984). Volumetric ($mg \cdot m^{-3}$) and areal ($mg \cdot m^{-2}$) expressions were used for TP and Chl *a*; the areal expressions were calculated as the product of TP and Chl *a* concentrations in the euphotic zone and the depth of the euphotic zone. To construct a general model to predict WODR, we combined data (i.e. WODR, $\bar{z}$, TP, and Chl *a*) from other temperate zone lakes (Schindler 1971; Dillon and Rigler 1974; Reid et al. 1975; Welch et al. 1976; Barica et al. 1978; Barica and Mathias 1979) with data from this study and analyzed these by regression with the BMDP statistical package program P1R (Dixon 1981). Other statistical analyses were from Snedecor and Cochran (1980) or Prepas (1984). All values in this report, except where noted, are expressed as means ± standard error.

To evaluate the differences between predictions of WODR with summer AHOD models and WODR models, we compared the residual mean squares (RMS) for each of four AHOD models with the RMS for the WODR model(s). The RMS for each model was calculated as follows:

$$RMS = \sum_{i=1}^{n} (pred_i - obs_i)^2/df$$

where $pred_i$ is the predicted WODR (from the AHOD model) and obs_i is the observed WODR for each lake (i) and df is the degrees of freedom. For each model, df was defined as the number of data points minus 1 minus the number of independent variables in the model.

Results

Fall Turnover

Just prior to freeze-up, DO levels were surprisingly low in 12 of the 13 study lakes; the average oxygen saturation level was 69% at the time of freeze-up, with values as low as 51%. Only one lake, Hasse, was almost fully saturated (94%) (Table 1). These findings are contrary to observations in other areas; e.g. in the pothole lakes of Manitoba, oxygen saturation levels are 80–100% just prior to freeze-up (Barica and Mathias 1979). Jackson and Lasenby (1982) reported that the maximum volume-weighted oxygen content of the Ontario lakes that they studied was achieved approximately 15 d after freeze-up; this is not the case in the Albertan lakes. In only 4 of the 13 lakes did the saturation level increase between the time of freeze-up and the first sampling date, possibly due to high oxygen consumption relative to the inputs of oxygen via freezeout and photosynthesis. Not only were DO levels low in the study lakes in the fall, but mixing was incomplete in two of them. A layer of anoxic water up to 5 m high remained over at least 18% of the sediments in the deepest part of Twin Lake. In Hubbles Lake, up to 9 m of water, overlying 15% of the sediments, was anoxic. Since oxygen consumption in lakes is mainly caused by bacteria at the sediment–water interface (Brewer et al. 1977), incomplete circulation could reduce oxygen depletion rates. Consequently, for the subsequent analyses, WODR for Twin and Hubbles lakes were not pooled with those from the remaining 11 study lakes where DO levels were above zero over the entire sediment area prior to freeze-up.

TABLE 1. Percent oxygen saturation in 13 Alberta lakes during fall and early winter, 1982. Measured oxygen saturation on the last visit before freeze-up (Prior), the first visit after freeze-up (Post), and predicted oxygen saturation on date of freeze-up were calculated from the *Y*-intercept of the regression of transformed oxygen mass against time (Predicted). Numbers in parentheses refer to the number of days before or after freeze-up when the lake was visited.

	% Oxygen saturation		
	Measured		
Lake	Prior	Post	Predicted
Amisk N	64(5)	64(21)	66
Amisk S	52(1)	54(21)	55
Baptiste S	58(5)	67(21)	70
Eden	62(1)	72(12)	67
Halfmoon	48(11)	55(9)	64
Hasse	94(9)	97(11)	97
Hubbles[a]	53(12)	54(9)	55
Lessard	65(19)	82(14)	77
Nakamun	60(9)	52(12)	52
Peanut	66(21)	70(7)	68
Sauer	72(11)	72(10)	77
Twin[a]	47(4)	59(12)	51
Wizard	88(9)	67(15)	81

[a]Lake did not mix to the bottom at fall turnover.

Lake Cover and Chlorophyll *a*

During the visits to the lakes while they were ice-covered, ice thickness at the sampling sites averaged 44.1 ± 1.35 cm (average maximum ice thickness was 60.5 ± 0.55 cm) and average snow depth was 8.2 ± 0.94 cm. White ice was noted only on Twin Lake; it was 2.5 cm deep. The total snowfall at Edmonton International Airport during the winter of 1982–83 was 0.92 m, which was lower (*t*-test, $P < 0.001$) than the previous 30-yr average (1.25 m) (Environment Canada 1953–83). Consequently, the potential for light entering the lakes during the winter of 1983 was greater than during an average winter in Alberta.

In 12 of the study lakes, Chl *a* concentration in the top 4 m decreased with the onset of ice-cover and remained low until

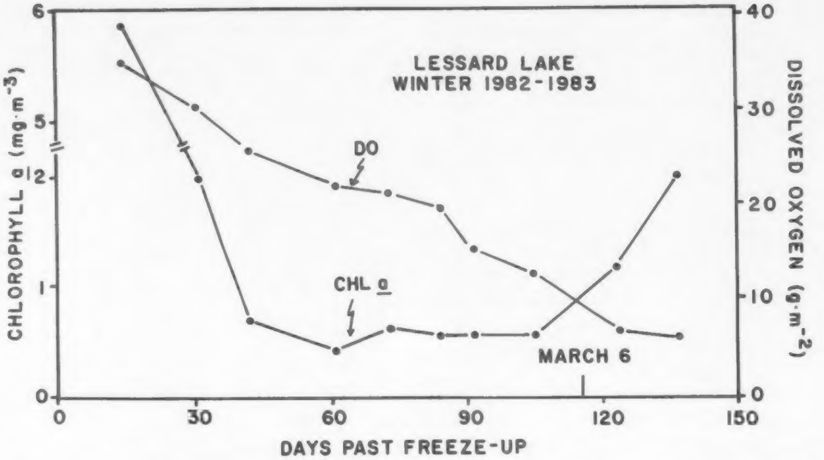

FIG. 1. Average chlorophyll *a* (Chl *a*) (●) in the top 4 m of Lessard Lake and whole-lake mass of dissolved oxygen (DO) (○) during the winter of 1982–83.

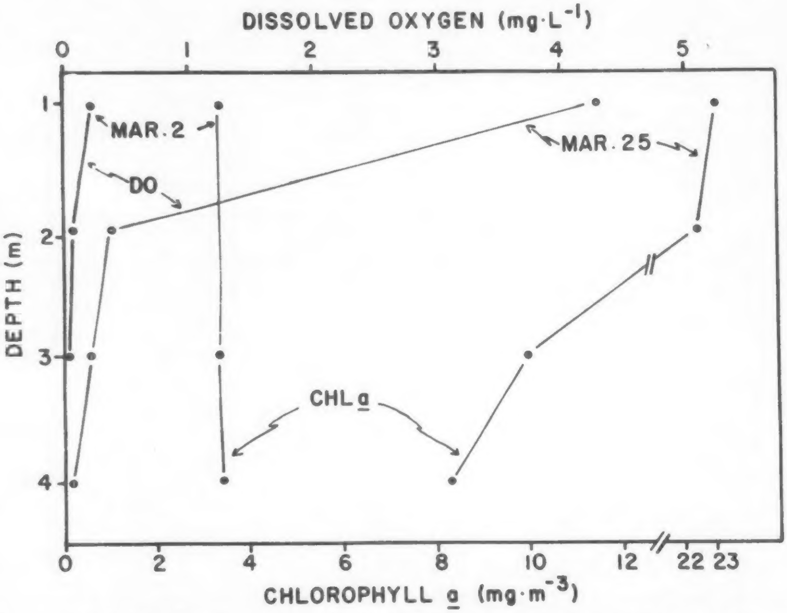

FIG. 2. Vertical distribution of chlorophyll *a* (Chl *a*) (●) and dissolved oxygen (DO) (○) in the top 4 m of Sauer Lake on the last two sampling dates (March 2 and March 25) in 1983.

late February or early March, as illustrated with data from Lessard Lake (Fig. 1). In these 12 lakes, average Chl *a* concentration in the top 4 m between freeze-up and 6 March, 1983, was $2.9 \pm 0.6\,\mathrm{mg \cdot m^{-3}}$ whereas after 6 March it rose to $4.6 \pm 1.4\,\mathrm{mg \cdot m^{-3}}$. For the same lakes, average snow depth during these two periods was 7.3 ± 0.9 cm and 10.3 ± 1.2 cm, respectively. In the 13th lake, Halfmoon, a bloom of algae (32 mg Chl $a \cdot \mathrm{m^{-3}}$) was recorded at a depth of 1 m on December 14 but decreased to 3 mg Chl $a \cdot \mathrm{m^{-3}}$ 10 d later. This algal bloom could have introduced oxygen under the ice but the DO level at 1 m below the surface decreased from $6.6\,\mathrm{mg \cdot L^{-1}}$ on December 14 to $4.8\,\mathrm{mg \cdot L^{-1}}$ on December 24. Snow cover on Halfmoon Lake for these same two dates was 4 and 5 cm, respectively. In March 1983, DO and Chl *a* levels increased in the top few metres in 10 of the lakes, as illustrated in Fig. 2 with data from Sauer Lake. In Sauer Lake, Chl *a* increased 5-fold (from 3.3 to $15.8\,\mathrm{mg \cdot m^{-3}}$) in the top 4 m, while DO increased 18-fold (from 0.06 to $1.2\,\mathrm{mg \cdot L^{-1}}$) in the same stratum between March 2 and 25, 1983. Since DO and Chl *a* levels began systematic increases under ice only after early March 1983, photosynthesis probably contributed an insignificant amount to oxygen levels between freeze-up and early March 1983.

Dissolved Oxygen

For the first 112 d past freeze-up, the mass of DO ($\mathrm{g \cdot m^{-2}}$) decreased in all lakes. Beginning in early March, changes in the

TABLE 2. Winter oxygen depletion rates (WODR) ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$) during the first 112 d past freeze-up and correlation coefficients, r, for the mass of oxygen (on linear and transformed, $X' = X^{0.65}$, data) versus days past freeze-up. All, rate covering entire 112-d period; early, rate based on first three sampling dates; later, rate based on remaining dates; trans, rate calculated on all data transformed. Sample size is indicated in parentheses.

	WODR				r	
Lake	All	Early	Later	Trans	All	Trans
Amisk N	0.554(5)	–	–	0.0877	0.98	0.99
Amisk S	0.848(5)	–	–	0.1162	0.98	0.99
Baptiste S	0.775(5)	–	–	0.1180	0.99	0.99
Eden	0.331(7)	0.481(3)	0.286(4)	0.0582	0.99	1.00
Halfmoon	0.462(6)	0.373(3)	0.448(3)	0.1352	0.99	0.98
Hasse	0.373(6)	0.426(3)	0.315(3)	0.0799	1.00	1.00
Hubbles[a]	0.475(7)	0.345(3)	0.520(4)	0.0846	0.99	0.99
Lessard	0.243(8)	0.342(3)	0.222(5)	0.0518	0.99	0.99
Nakamun	0.281(10)	0.587(3)	0.184(7)	0.0773	0.96	0.98
Peanut	0.405(7)	0.512(3)	0.363(4)	0.0881	1.00	1.00
Sauer	0.363(6)	0.428(3)	0.271(3)	0.0988	0.99	1.00
Twin[a]	0.193(5)	–	–	0.0258	0.99	0.99
Wizard	0.533(5)	–	–	0.1052	0.99	0.99

[a] Lake did not mix to bottom at full turnover.

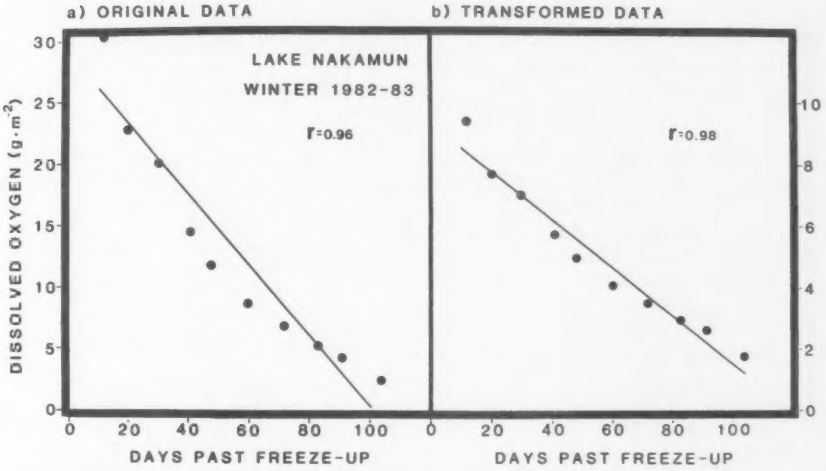

FIG. 3. Areal mass of dissolved oxygen in Lake Nakamun during the first 112-d past freeze-up in 1982–83. (a) Original data (X); (b) transformed ($X' = X^{0.65}$) data. Linear regression lines are drawn through both sets of data; r = correlation coefficient.

mass of DO followed two distinct patterns: in three lakes DO increased, while in the remaining 10 lakes it continued to decrease, but at a lower rate than previously. Since DO levels decreased in all lakes during the first 112 d past freeze-up and during the same period there was no evidence that a significant amount of oxygen was added to the lakes via photosynthesis, WODR were calculated for this 112-d period.

Winter oxygen depletion rates, although systematic, were not linear during the 112-d period; rather, WODR were more rapid earlier than later in this period. To illustrate this pattern, we analyzed the first 112-d period on the seven lakes where (1) data were sufficient to allow the 112-d period to be described by two independent regression lines (i.e. $n \geqslant 6$) and (2) the lake had mixed to the bottom at fall overturn. To calculate independent regression lines of WODR versus time for the earlier and later portions of the 112-d period, the data for each of the lakes were divided into (1) the first three sampling dates (early) and (2) the remaining sampling dates (later). For six of the seven lakes, the WODR for the early period were consistently higher than rates for the later period, and the differences for all seven lakes were statistically significant (Wilcoxon signed-rank test, $P < 0.05$) (Table 2), suggesting that oxygen was depleted in a nonlinear fashion. Data from the lake where we had the most data points (Nakamun) are used to illustrate the WODR patterns in most Albertan lakes (Fig. 3). These results were surprising; WODR are usually treated as linear processes as long as average whole-lake DO levels remain above $3\ mg \cdot L^{-1}$ (Mathias and Barica 1980). Our data do not support this hypothesis; e.g. in two lakes, Lessard and Eden, average whole-lake DO levels remained above 3.6 and $4.0\ mg \cdot L^{-1}$, respectively, during the

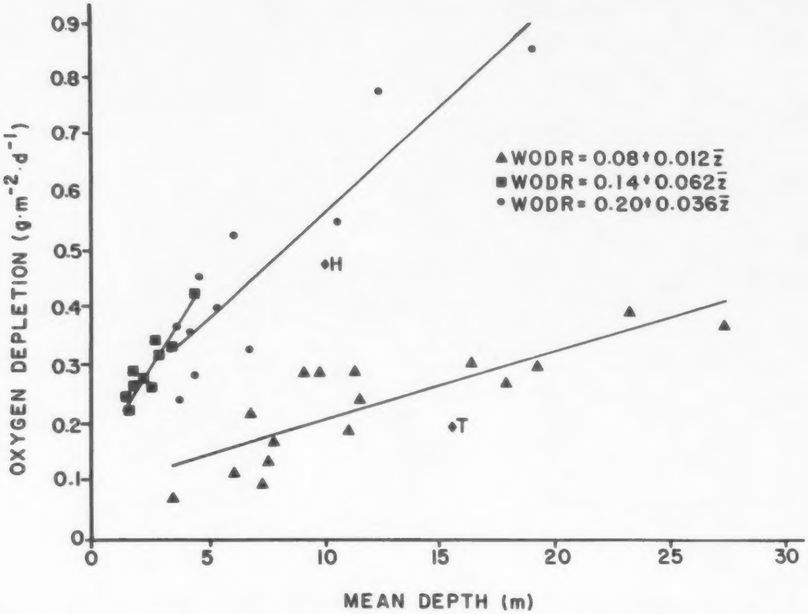

FIG. 4. Relationship between winter oxygen depletion rates (WODR) and mean depth ($\bar{z}$) for three sets of temperate zone lakes in Canada. ▲, Welch et al. (1976); ■, Barica and Mathias (1979); ●, this study. Hubbles Lake (◆H) and Twin Lake (◆T) are part of this study but are not included in the regression analysis.

112-d period when WODR were calculated. Yet in these same lakes, WODR just after freeze-up were 54 and 68% higher, respectively, than later in the 112-d period (Table 2). Thus, in this study, WODR appear nonlinear regardless of DO levels.

Since changes in the mass of DO appear nonlinear in the study lakes, the data were transformed prior to the calculation of WODR. The best transformation for the mass of DO (X) versus time was a power function: $X' = X^{0.65}$. For 12 of the 13 lakes, the correlation between the transformed DO data and days past freeze-up was better than or equal to the correlation based on the untransformed data (Table 2; Fig. 3). Data from this study and Jackson and Lasenby (1982) suggest that winter oxygen depletion may be a nonlinear process. Both of these studies were based on a relatively large number of data points (5–19). These observations indicate that even more data are required on individual lakes to properly characterize the oxygen depletion–time relationship under ice-cover.

We examined the relationship between two morphometric parameters ($\bar{z}$ and Z_{max}), four parameters used as estimates of annual production of organic matter (LOI, spring TP, summer TP, and summer Chl *a* levels), and WODR based on the transformed data (Table 3). Winter oxygen depletion rates based on transformed data (WODR′) were positively correlated with all variables except LOI. The significant negative relationship between LOI and WODR′ is hard to explain. Surprisingly, the only positive significant relationships were between estimates of open-water productivity (TP and Chl *a*) and WODR′ (Table 3); the best predictors of WODR′ were summer TP (TP_{su}) and Chl *a* in $mg \cdot m^{-2}$:

(1) $WODR' = 0.005 + 0.00047\,TP_{su}$

(2) $WODR' = 0.062 + 0.00052$ Chl *a*.

TABLE 3. Correlation coefficients for winter oxygen depletion rates ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$), both transformed ($X' = X^{0.65}$) and linear data versus six characteristics in Alberta lakes: mean depth ($\bar{z}$), maximum depth (Z_{max}), loss on ignition (LOI), spring and summer total phosphorus (TP_{sp} and TP_{su}), and summer chlorophyll *a* (Chl *a*). Phosphorus and chlorophyll are expressed per unit area of the lake and per unit volume of the trophogenic zone. Significant correlations: $*P < 0.05$; $**P < 0.01$; $***P < 0.005$.

Characteristic	Transformed	Linear
$\bar{z}$ (m)	0.41	0.90***
Z_{max} (m)	0.36	0.82**
LOI (%)	−0.72*	−0.36
TP_{sp} ($mg \cdot m^{-2}$)	0.46	0.73**
TP_{su} ($mg \cdot m^{-2}$)	0.72*	0.64*
Chl *a* ($mg \cdot m^{-2}$)	0.72*	0.37
TP_{sp} ($mg \cdot m^{-3}$)	0.68*	0.23
TP_{su} ($mg \cdot m^{-3}$)	0.46	0.01
Chl *a* ($mg \cdot m^{-3}$)	0.40	−0.09

These results are contrary to investigations on two other groups of lakes (Welch et al. 1976; Barica and Mathias 1979) where DO data were not transformed prior to calculating WODR. In the other investigations, morphometric parameters were much better predictors of WODR than estimates of summer productivity, whereas summer productivity was the best estimator of WODR′ in this study.

Since our WODR data are the first to be treated as a nonlinear process, they cannot be compared as such with other regional data sets. Thus, to compare and combine our data with these other regional data sets we also calculated WODR for the

TABLE 4. Deviations of predicted winter oxygen depletion rates (WODR) from observed WODR for 11 Alberta lakes. The predicted values are based on six models listed below: two WODR models (1 and 2) and four summer areal hypolimnetic oxygen depletion (AHOD) models (3, 4, 5, and 6). RMS is the residual mean square associated with the model, and df is the degrees of freedom associated with each model —, WODR were not calculated, since mean summer Secchi disc depth (SD) is less than 1 m; $\bar{z}$, mean depth; TP, mean summer total phosphorus in the euphotic zone; Chl *a*, mean summer chlorophyll *a* in the euphotic zone; *t* = mean lake temperature under ice-cover (modified from the original expression where *t* was $(t - 4)$).

Lake	Model					
	1	2	3	4	5	6
Amisk N	−0.345	0.253	−0.085	−0.050	0.139	−0.212
Amisk S	−0.535	0.502	−0.254	−0.158	0.326	−0.562
Baptiste S	−0.544	0.149	−0.243	−0.287	0.040	−0.360
Eden	−0.168	0.242	−0.030	−0.074	−0.011	0.312
Halfmoon	−0.325	−0.025	0.079	0.088	0.019	1.503
Hasse	−0.248	−0.004	−0.116	−0.150	−0.127	0.172
Lessard	−0.116	0.141	0.037	0.084	0.131	0.058
Nakamun	−0.152	0.131	0.261	—	0.195	—
Peanut	−0.261	0.076	−0.109	−0.175	−0.078	0.226
Sauer	−0.233	0.036	−0.083	−0.174	−0.099	0.327
Wizard	−0.379	−0.008	−0.072	0.079	0.021	−0.278
RMS	0.1322	0.0491	0.0306	0.0313	0.0308	0.3894
df	9	9	8	7	7	9

1. $\mathrm{WODR} = 0.08 + 0.012\bar{z}$ (Welch et al. 1976)
2. $\mathrm{WODR} = 0.14 + 0.062\bar{z}$ (Barica and Mathias 1979)
3. $\log_{10}\mathrm{AHOD} = 1.52 + 0.48 \log_{10}(\mathrm{TP}) + 0.38 \log_{10}(\bar{z})$ (Cornett and Rigler 1980)
4. $\log_{10}\mathrm{AHOD} = 2.45 - 0.67 \log_{10}(\mathrm{SD}) + 0.47 \log_{10}(\bar{z})$ (Cornett and Rigler 1980)
5. $\mathrm{AHOD} = \dfrac{3.8(1.15(\mathrm{Chl}\ a)^{1.33})\cdot\bar{z}\cdot 2^{(t/10)}}{(9 + 1.15(\mathrm{Chl}\ a)^{1.33})\cdot(50 + \bar{z})} + \dfrac{0.12(1.15(\mathrm{Chl}\ a)^{1.33})}{9 + 1.15(\mathrm{Chl}\ a)^{1.33}}$ (modified from Charlton 1980)
6. $\log_{10}\mathrm{AHOD} = -1.37 \log_{10}(\mathrm{SD}) - 0.65$ (Lasenby 1975)

Albertan lakes based on untransformed data. These WODR calculated from the original data for Albertan lakes are used in the subsequent calculations and discussion.

In the 11 Albertan lakes that mixed at fall overturn, WODR covered almost twice the range, $0.243–0.848\ \mathrm{g\ O_2 \cdot m^{-2} \cdot d^{-1}}$, observed in the two previous studies on WODR in Canada (Fig. 4). The WODR for these Albertan lakes were tested against existing empirical models. The model for lakes on the Precambrian Shield, which are similar in depth but less productive (Welch et al. 1976), consistently underestimated WODR in the Albertan lakes (Wilcoxon signed-rank test, $P < 0.01$). Conversely, the model for the generally shallower prairie pothole lakes (Barica and Mathias 1979) consistently overestimated WODR in the Albertan lakes (Wilcoxon signed-rank test, $P < 0.05$) (Table 4; Fig. 4).

To compare WODR in Albertan lakes with the lakes on the Precambrian Shield and in southern Manitoba, WODR in the Albertan lakes were regressed against parameters indicative of lake morphometry and productivity (Table 3). Based on untransformed data, patterns in the Albertan lakes were comparable with the studies in other regions (Welch et al. 1976; Barica and Mathias 1979); morphometry was a stronger predictor of WODR than estimates of productivity. The best predictor of WODR was mean depth ($\bar{z}$ in m):

$$(3)\quad \mathrm{WODR} = 0.20 + 0.036\bar{z}.$$

Unfortunately, too few Albertan lakes were sampled to construct multiple regressions on these data alone. Productivity, as estimated by spring and summer TP, was significantly correlated with WODR only when TP was expressed on an areal basis. Thus, all further calculations are based on areal expressions of productivity estimates.

A serious limitation with the existing models to predict WODR is that they work only in the region where they were developed. These published models to predict WODR are based only on morphometry (Welch et al. 1976; Barica and Mathias 1979). However, there are numerous suggestions that oxygen depletion rates are a function of both $\bar{z}$ and lake productivity (Table 3, this study; Mathias and Barica 1980; Charlton 1980; Cornett and Rigler 1980). Previously, data were insufficient to test whether a model including both morphometry and estimates of productivity (1) could be developed to predict WODR and (2) would be generally applicable to north temperate zone lakes.

To develop a model to predict WODR over a wide range of lake types, estimates of WODR, open-water productivity, and morphometry from 48 lakes in Alberta, central and northwestern Ontario, and Manitoba (Table 5) were combined. These lakes covered a broad range in terms of mean depth ($1.5 \leq \bar{z} \leq 22.7$ m) and estimates of summer productivity ($2 \leq \mathrm{Chl}\ a \leq 184\ \mathrm{mg \cdot m^{-2}}$ and $24 \leq \mathrm{TP} \leq 222\ \mathrm{mg \cdot m^{-2}}$) in the euphotic zone. Unfortunately, TP data were not collected for the Manitoban lakes and TP estimates were available for only six lakes in northwestern Ontario. In the combined data set, WODR were strongly correlated with estimates of lake productivity and morphometry (Table 6). However, contrary to the results reported for regional data sets (excluding the transformed data set for the Albertan lakes), estimates of productivity were stronger single predictors of WODR than morphometry. Thus, morpho-

TABLE 5. Winter oxygen depletion rates (WODR) ($g\ O_2 \cdot m^{-2} \cdot d^{-1}$), mean depth ($\bar{z}$), total phosphorus (TP) ($mg \cdot m^{-2}$), and chlorophyll *a* (Chl *a*) ($mg \cdot m^{-2}$) from four sets of temperate zone lakes in Canada.

Lake	WODR	$\bar{z}$	Spring TP	Summer TP	Summer Chl *a*
Alberta[a]					
Amisk N	0.554	10.7	502	222	61
Amisk S	0.848	19.4	422	219	86
Baptiste S	0.775	12.6	320	202	64
Eden	0.331	6.9	223	177	27
Halfmoon	0.462	4.8	257	215	147
Hasse	0.372	3.7	199	174	26
Lessard	0.243	3.9	115	97	42
Nakamun	0.285	4.5	181	135	72
Peanut	0.407	5.5	260	211	37
Sauer	0.363	4.2	265	208	28
Wizard	0.533	6.2	235	192	64
Central Ontario[b,c,d]					
Beech	0.282	9.8	81	73	10
Bob	0.273	18.0	100	79	14
Boshkung	0.393	23.4	88	69	14
Cameron	0.217	7.1	83	88	14
Cranberry	0.075	3.5	70	83	11
Eagle	0.169	7.9	92	76	22
Four Mile	0.282	9.3	124	98	16
Green	0.117	6.1	91	87	16
Haliburton	0.295	19.6	82	58	12
Halls	0.373	27.2	71	63	13
L. Boshkung	0.127	7.6	80	59	19
Maple	0.242	11.6	72	79	11
Moose	0.295	16.6	77	73	13
Oblong	0.186	11.2	73	66	25
Pine	0.097	7.4	71	85	13
Twelve Mile	0.286	11.5	76	68	16
Northwest Ontario[e,f,g]					
122	0.253	7.2			24
132	0.110	3.3			17
227	0.223	4.4		73	16
230	0.138	6.2			41
239	0.186	10.5		74	11
240	0.199	6.1		50	7
261	0.045	2.9			9
265	0.171	9.8			18
303	0.036	1.5		24	2
304	0.236	3.2		71	3
305	0.207	15.1		92	11
Manitoba[h,i]					
885	0.260	1.8			184
882	0.270	2.1			90
255	0.290	1.8			37
318	0.220	1.6			64
587	0.260	2.5			53
721	0.240	1.6			26
675	0.340	2.7			55
200	0.320	2.8			54
019	0.330	3.4			49
Nora	0.420	4.2			57

[a] Data on TP and Chl *a* for Nakamun and Halfmoon lakes from Riley (1983); all other TP and Chl *a* data from Prepas and Vickery (1984).

[b] Data on WODR from Welch et al. (1976).

[c] Data on spring TP and summer Chl *a* from Dillon and Rigler (1974).

[d] Data on summer TP from P. J. Dillon (Ontario Ministry of Natural Resources, unpubl. data).

[e] Data on WODR from Schindler (1971).

[f] Data on summer TP from Reid et al. (1975) and G. Linsey (Freshwater Institute, Winnipeg, Man., pers. comm.).

[g] Data on summer Chl *a* from Armstrong and Schindler (1971) and Reid et al. (1975).

[h] Data on WODR from Barica and Mathias (1979).

[i] Data on summer Chl *a* from Barica et al. (1978) and Mathias and Barica (1980).

metric variables are good predictors of WODR within regions where lake productivity levels are moderately similar; however, between regions where lake productivity levels differ markedly, productivity is the strongest predictor of WODR.

Next, we combined $\bar{z}$ with the productivity estimates to examine whether a multiple regression would improve on the linear models to predict WODR. In all cases the inclusion of estimates of both open-water productivity and morphometry improved the WODR models (Table 6). In each multiple regression, the estimate of open-water productivity explained more of the variation in WODR than morphometry. The WODR model based on summer TP ($mg \cdot m^{-2}$) and $\bar{z}$ had the highest correlation:

$$(4)\quad \text{WODR} = -0.101 + 0.00247\ \text{TP}_{su} + 0.0134\bar{z}.$$

However, TP data were available for fewer lakes than Chl *a*. When regressions were run on the lakes where summer TP data were available, but incorporating WODR, Chl *a*, and $\bar{z}$ in the regression, the correlation was highly significant ($r = 0.78$, $P < 0.0001$) but lower than when summer TP was used. Thus, summer TP is a better predictor of WODR than Chl *a*. However, models based on $\bar{z}$ and some estimate of productivity, TP or Chl *a*, can be used to predict WODR over a wide range of lakes in north temperate regions.

One-Site-Sampling

In the five lakes where DO profiles were taken at more than one site, considerable horizontal variation in DO levels was found. There was no consistent pattern in the DO profiles at the various stations; depth at site sampled did not influence DO levels. For instance, on January 22, 1983, in Lessard Lake at a depth of 1 m, DO concentration increased from 7.4 $mg \cdot L^{-1}$ at the site of maximum depth to 9.6 $mg \cdot L^{-1}$ at the site where the depth was only 1 m, whereas on January 9, 1983, in Halfmoon Lake at a depth of 1 m, DO decreased from 2.1 $mg \cdot L^{-1}$ at the site of maximum depth to 0.9 $mg \cdot L^{-1}$ at the site where the depth was only 1 m. To illustrate the possible error when only one site is sampled and the whole-lake oxygen mass is based on that site, oxygen profiles collected at six sites in Wizard Lake on March 7, 1983 (Table 7) were used. To estimate DO mass for the whole lake based on all the sampling sites, DO mass was calculated for each site and summed together. To calculate the mass of oxygen at each site, we divided the volume of each stratum by the number of samples taken at that stratum depth. The DO concentration of each sample from each site was multiplied by the corresponding volume associated with the sample, and all were summed together to provide the whole-lake oxygen mass. Whole-lake oxygen mass was divided by the volume of the lake to yield average oxygen concentration. The average DO value

TABLE 6. Regression analysis of winter oxygen depletion rates (WODR) ($g\,O_2\cdot m^{-2}\cdot d^{-1}$) versus four parameters: mean depth ($\bar{z}$), spring and summer total phosphorus (TP_{sp} and TP_{su}) ($mg\cdot m^{-2}$), and summer chlorophyll *a* (Chl *a*) ($mg\cdot m^{-2}$) for the lakes in Table 5 (n = number of lakes used in each regression; r = correlation coefficient of each regression; significant correlations: $^{*}P < 0.05$; $^{**}P < 0.005$; $^{***}P < 0.001$).

Parameter	*n*	Equation	*r*
$\bar{z}$	48	$WODR = 0.214 + 0.00894\bar{z}$	0.34*
TP_{sp}	27	$WODR = 0.124 + 0.00128TP_{sp}$	0.81***
TP_{su}	33	$WODR = 0.052 + 0.00227TP_{su}$	0.77***
Chl *a*	48	$WODR = 0.212 + 0.00201\ \text{Chl}\ a$	0.44**
TP_{sp}, $\bar{z}$	27	$WODR = -0.001 + 0.00134TP_{sp} + 0.0119\bar{z}$	0.89***
TP_{su}, $\bar{z}$	33	$WODR = -0.101 + 0.00247TP_{su} + 0.0134\bar{z}$	0.90***
Chl *a*, $\bar{z}$	48	$WODR = 0.093 + 0.00257\ \text{Chl}\ a + 0.0127\bar{z}$	0.65***

TABLE 7. Dissolved oxygen ($mg\cdot L^{-1}$) profiles at six sampling sites on Wizard Lake, March 7, 1983.

Depth (m)	Site					
	1	2	3	4	5	6
1	3.22	5.95	2.75	4.82	5.15	4.16
2	2.24	3.91	2.25	3.89	4.16	3.50
3	1.97	3.73	2.04	3.59	3.85	
4	1.89	3.37	1.24	3.21	3.35	
5	1.30	3.25	1.11	2.86	3.22	
6	0.89	2.00	0.90	2.75		
7	0.89	2.11	0.69			
8	0.38	1.41	0.87			
9	0.22					
10	0.08					
11	0.05					

was 47% higher when data from all stations were used rather than data from the site of maximum depth (2.2 and 1.5 $mg\cdot L^{-1}$, respectively).

To further illustrate the possible errors that could result when whole-lake oxygen mass is calculated from data collected at only one site, three separate estimates of oxygen mass ($g\cdot m^{-2}$) were made for the upper 8 m of Wizard Lake. At each station that was a minimum of 8 m deep, the DO concentration at each depth was multiplied by the whole-lake stratum volume corresponding to the depth of the sample. The results were summed to yield oxygen mass in the upper 8 m and divided by the under-ice surface area. Oxygen mass calculated in this manner ranged from 8.1 to 16.8 $g\cdot m^{-2}$; the main station had 8.5 $g\cdot m^{-2}$. Thus, it appears that sampling at more than one site would improve estimates of whole-lake oxygen mass over one-site-sampling for Albertan lakes. However, in all sampling programs, a trade-off must be made between the number of lakes sampled during the winter and the number of sites sampled on a lake at each visit.

Discussion

Previous authors (Welch et al. 1976; Barica and Mathias 1979; Mathias and Barica 1980) have reported that WODR are linear throughout the winter as long as average lake DO remains above anywhere from 1 to 3 $mg\cdot L^{-1}$. Data from this study and Jackson and Lasenby (1982) do not support the generality of this observation. One possible explanation for the apparent nonlinearity of these data, in addition to the relatively large number of data points per lake, is that WODR for the Albertan lakes are based on a longer time interval than previous studies on other temperate zone lakes in Canada. The WODR for the prairie pothole lakes were based on approximately 90 d (Barica and Mathias 1979) as were the WODR for the Ontario lakes (Welch et al. 1976). The nonlinear trends in WODR in this study can be explained in part by the change in the rate of supply of oxygen to the sediments. Since oxygen depletion rates are greatest at the sediment–water interface, whole-lake oxygen depletion is, in part, governed by the rate of oxygen supply to the sediments. This rate is a function of the distance to the sediments from water containing oxygen and the DO concentration in this water:

$$\text{Oxygen flux rate} = K\cdot(\text{oxygen concentration gradient})$$

where K is the eddy diffusion constant (Mathias and Barica 1980). All of the Albertan lakes that mixed to the bottom at fall overturn developed clinograde oxygen profiles during the winter (Fig. 5). As the winter progressed, the DO in the lake decreased, the distance from the sediments to water containing DO increased, and thus the oxygen flux rate could have also decreased. Methods to accurately measure the movement of oxygen from open water to the sediment–water interface need to be developed to assess the effect(s) of changing rates of oxygen supply on WODR. Another possible explanation for nonlinear WODR is that some organic material in the sediments is more easily oxidized and is used up first (Edberg 1976; Jackson and Lasenby 1982).

To obtain better estimates of the oxygen content in lakes, we suggest that DO samples should be collected at several stations. Further research is needed to determine the extent, magnitude, and cause(s) of spatial heterogeneity of DO profiles in lakes under ice-cover. Some likely causes are (1) groundwater entering the lake, (2) differential oxygen depletion at various sites in the lake (Linsey 1981), and (3) localized inputs of oxygen to the lake.

Jackson and Lasenby (1982) constructed two models that predict oxygen profiles in lakes under ice-cover: one model for lakes situated on the Precambrian Shield and another for lakes situated in limestone basins. These models are based on the oxygen concentrations in the lake 5–15 d after freeze-up. The two models were tested against the Albertan lake data. The model developed for lakes located on the Precambrian Shield consistently overestimated the final DO levels in the Albertan lakes by an average of 2.5 $mg\cdot L^{-1}$; conversely, the model for the lakes in limestone basins consistently underestimated the final oxygen levels by an average of almost 2.0 $mg\cdot L^{-1}$. An underlying assumption of these models is that lakes in limestone

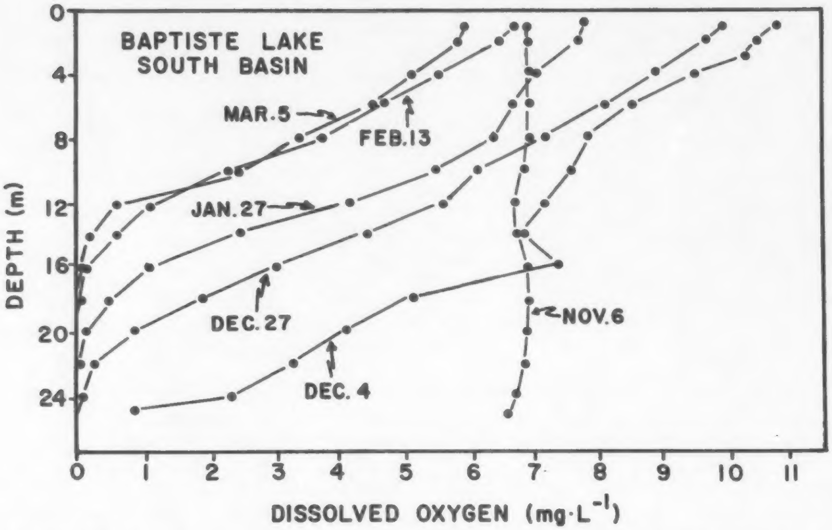

FIG. 5. Dissolved oxygen profiles from Baptiste Lake, South Basin, during the fall and winter of 1982–83.

basins are more productive than those on the Precambrian Shield; hence, DO is depleted faster in the limestone basin lakes. Jackson and Lasenby's (1982) model for lakes on the Precambrian Shield is based on only five lakes where the maximum depth ranges from 8 to 33 m and average summer Chl *a* is approximately 2 mg·m^{-3}. The model developed for lakes in limestone basins is based on only three lakes where the maximum depth ranges from 16 to 18 m; summer productivity estimates are not available for these lakes; however, they are probably more productive than the lakes on the Precambrian Shield but less productive than the Albertan lakes. Since the Albertan lakes are more productive than Ontario lakes, both on the Precambrian Shield and in limestone basins (mean summer Chl *a* concentration (mg·m^{-3}) in 19 Ontario lakes was 1.4 (Dillon and Rigler 1974) and in 27 Albertan lakes was 26.5 (Prepas and Trew 1983)), we expected that both models would predict higher final oxygen levels than observed in the Albertan lakes, but they did not. Possibly, with a larger data set, a more general model, including an estimate of productivity, could be developed to predict DO profiles under ice-cover.

If the same processes are influencing WODR and summer AHOD, AHOD models may predict WODR. Four AHOD models were chosen and tested with WODR data from the Albertan lakes. The four AHOD models chosen require inputs that were available for the Albertan lakes: estimates of open-water productivity (Secchi disc depth, summer TP, and Chl *a* levels), morphometry ($\bar{z}$), and water temperature (Lasenby 1975; Charlton 1980; Cornett and Rigler 1980). To assess the accuracy with which the AHOD models predicted WODR, we compared the RMS from the predicted WODR and the observed WODR for the 11 Albertan lakes (Table 4) with the RMS from the $\bar{z}$–WODR model for the Albertan lakes (Eq. 3, RMS = 0.0078). The RMS for the AHOD models were 4–50 times greater than for Eq. 3. To determine how well AHOD models predicted WODR over a broad range of lake types, the RMS from the summer TP – $\bar{z}$ – WODR model for temperate lakes (Eq. 4, RMS = 0.0065) was compared with the RMS for the two AHOD models of Cornett and Rigler (1980). For this comparison the same lakes were used as in the construction of Eq. 4. The RMS for model 3 (Table 4) based on mean summer TP and mean depth was 0.0124 and the RMS for model 4 (Table 4) based on mean summer Secchi disc depth and mean depth was 0.0137. The RMS for the two AHOD models are approximately twice as great as for Eq. 4. Thus, it appears that similar factors influence summer and winter oxygen depletion models. However, an independent data set is needed to clarify whether the $\bar{z}$ – summer productivity – oxygen depletion rate relationship is identical under ice-cover and in the hypolimnion of a stratified lake.

The most important parameter in the models to predict WODR and AHOD over a broad range of lake types are estimates of open-water productivity (summer TP or Chl *a*) (Table 6, this study; Cornett and Rigler 1980; Charlton 1980). Both WODR and AHOD are influenced by morphometry but to a lesser degree than productivity. Summer hypolimnetic oxygen depletion is also influenced by water temperature (Charlton 1980; Cornett 1981), and WODR could be as well, although sufficient data do not exist to test this hypothesis. Incorporating water temperature in equations to predict AHOD is warranted, since there may be large temperature differences in the hypolimnia of various lakes in summer; Charlton (1980) reported values ranging from 4.0 to 11.0°C in the Laurentian Great Lakes. During ice-cover, the temperature variation between lakes is not as great as in lake hypolimnia during summer; mean winter volume-weighted temperatures ranged from 3.0 to 3.4°C in three lakes in Ontario (Jackson 1979) and from 2.2 to 3.4°C in the Albertan lakes. With such little variation between ice-covered lakes, the influence of water temperature on WODR is likely less than on AHOD.

The models presented to predict WODR over a broad range of lakes should be tested with independent data to determine their accuracy. Data from lakes with productivity–morphometry relationships different from those in Table 5, e.g. shallow and unproductive, are needed to improve the generality of the models presented.

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Hotelling's T^2 to Identify the Origin of Atlantic Salmon (*Salmo salar*) in a Mixed-Stock Fishery

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Reddin, D. G., and R. K. Misra. 1985. Hotelling's T^2 to identify the origin of Atlantic salmon (*Salmo salar*) in a mixed-stock fishery. Can. J. Fish. Aquat. Sci. 42: 250–255.

We used a new approach based on measurements of four scale characters, for identifying Atlantic salmon (*Salmo salar*) caught in the commercial fishery at St. Ann's Harbour, Nova Scotia, and that were returning to North River. Utilizing Hotelling's T^2, we compared the vector of observations of each member of the commercial sample (size = 29) with the vector of means of the sample from the angling fishery on North River (size = 48). Misclassification rate was estimated by the "leave-one-out" technique. The variables chosen for analysis were the measurements of the longest oral radii between each of the first three river and first sea annuli. The analysis indicated that 79–88% of the individuals in the commercial sample could have been migrating to North River. This technique is proposed for cases in which the requirement to have samples from all contributing stocks for discriminant analysis is not possible.

Les auteurs utilisent une nouvelle approche basée sur la détermination de quatre caractères scalimétriques dans le but d'identifier le saumon atlantique (*Salmo salar*) capturé par des pêcheurs commerciaux à St. Ann's Harbour (N.-É.) au cours de son retour à la rivière North. En se servant du T^2 de Hotelling, ils comparent le vecteur des observations effectuées sur chaque spécimen de la prise commerciale ($N = 29$) au vecteur de la moyenne de l'échantillon ($N = 48$) prélevé dans les captures sportives effectuées dans la rivière North. Ils évaluent le taux de classification erronée à l'aide de la technique d'exclusion d'une donnée. Les variables choisies pour l'analyse sont la longueur des plus longs radii oraux entre les trois premiers annuli produits en eau douce et le premier annulus produit en eau salée. L'analyse a démontré que de 79 à 88 % des individus composant la prise commerciale se dirigeaient peut-être vers la rivière North. On pourra utiliser la présente technique dans les cas où on ne peut obtenir d'échantillons de tous les stocks en vue d'une analyse discriminante.

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One of the greatest obstacles to the sound management of Atlantic salmon (*Salmo salar*) stocks is that most of the commercial fisheries exploiting them are situated on feeding grounds or on major migration routes (Saunders 1981). Most stock-assessment techniques such as general production or stock–recruitment models have, as a basic assumption, that catches as measures of abundance be from individual stocks (Ricker 1975). This assumption is clearly invalid for fisheries that harvest a number of stocks where they are mixed along migration routes or on feeding grounds. However, biologists are still required to assess the status of stocks for individual river systems and predict abundance of future runs to ensure adequate spawning escapement. This requires predictions of stock abundance prior to exploitation by fisheries so that managers can develop management strategies that equitably share harvests amongst all user groups. Empirical models such as currently utilized to set total allowable catch (TAC) for Atlantic salmon in the Baltic Sea (Anonymous 1982) could prove useful if coupled with discrimination techniques used to separate the component stocks of mixed-stock fisheries. As well, enhancement of stocks requires estimation of total production so that costs and benefits can be calculated.

The statistical technique most commonly used to identify populations or subpopulations of salmon stocks has been discriminant analysis of scale patterns. For Pacific salmonids, both parametric statistical techniques assuming that data are normally distributed (Amos et al. 1963; Anas and Murai 1969; Major et al. 1975; Bilton and Messinger 1975; Marshall et al. 1978; Scarnecchia and Wagner 1980) and nonparametric techniques that do not assume an underlying distribution (Cook and Lord 1978; Cook 1982) have been employed. For Atlantic salmon, Lear and Sandeman (1980) were able to distinguish, on the basis of scale characters, salmon of European and North American origin that were caught in the mixed-stock fishery at West Greenland. Lear and Misra (1978) showed that variations in scale characters of Atlantic salmon existed from south to north along the east coast of North America and suggested that these characters could be used to discriminate stock origins of Atlantic salmon in mixed-stock fisheries.

The results of Lear and Misra's (1978) work suggested that it may be possible to identify stocks or stock components in mixed-stock fisheries using discriminant analysis of scale patterns of Atlantic salmon. However, a requirement of the technique is that the unknown individuals to be identified come from one of the known groups (Reyment 1966). This requirement is difficult for Atlantic salmon because it assumes that an extensive knowledge of interception patterns in mixed-stock fisheries exists and then requires scale samples from each stock potentially harvested in the mixed-stock fishery. In the case of some mixed-stock fisheries for Atlantic salmon that may have as many as 400–500 stocks potentially contributing, this is clearly very difficult. Our objective was to consider an alternate solution to the problem by identifying in a mixed-stock fishery at a river mouth only those individuals caught in that fishery belonging to that river. North River, Nova Scotia, provided us with the data set necessary to investigate the technique, as it is known that salmon returning to North River and other Gulf of St. Lawrence rivers are caught in St. Ann's Harbour (L. Marshall, Department of Fisheries and Oceans, Fisheries Research Branch, Halifax, N.S., pers. comm.).

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Methods

Scales are a logical choice for separating stocks in mixed-stock fisheries, since they have been used to differentiate stocks of salmon caught on the high seas to continent of origin for both Pacific and Atlantic salmonids (Lear and Sandeman 1980; Major et al. 1975) and their use has been suggested for classifying Atlantic salmon to river of origin by Lear and Misra (1978). Scales were chosen over other body parts, as they are inexpensive, easy to collect and frequently available. Thus, scale samples were collected from salmon caught in the angling fishery (sample of "known" origin) in North River and in the commercial fishery (sample of "unknown" origin) in St. Ann's Harbour (Fig. 1). Fish were sampled randomly throughout the run in both commercial and angling fisheries from June to August of 1978. Commercial trap nets were used in St. Ann's Harbour, and since mainly multi-sea-winter salmon (virgin fish having spent two or three winters at sea) were caught, only fish of these ages were used in the sample from the angling fishery. The angling fishery is restricted to fly-fishing for only a short distance upstream, as much of the river is inaccessible to anglers (L. Marshall, pers. comm.). North River is a relatively small river both in terms of dimensions and salmon populations, as it is only 26 km in length and drains an area of 218 km^2. The angling catch in 1978 was 216 fish, only 10 of which were grilse (Mitham and Bernard 1978).

Other reasons we chose North River were because scale samples from both fisheries already existed and because the samples from the angling and commercial catches were of a size thought to be representative of the population in the river. In fact, the sample of 48 fish is 22% of the angling catch. Exploitation rates of 0.25–0.60 have been reported for rivers in this area of the Gulf of St. Lawrence, and whereas independent estimates are not published for North River, these rates suggest that the sample of 48 could represent between 6 and 13% of the adult returns to North River (Anonymous 1978). Another important aspect is that of size selectivity of fly-fishing gear to the population in the river. Studies on size selection in angling fisheries for Atlantic salmon are nonexistent; however, comparison of mean fork length of salmon caught in the angling fishery on Sand Hill River, Labrador (unpubl. data) with mean fork length of the total population of fish passing through a counting fence showed no significant differences ($F_{1,574} = 1.38$, $P = 0.24$). Thus, for Sand Hill River a sample taken from salmon caught in the angling fishery is representative of the population in that river. This was assumed to be the case for North River as well.

Scales were removed from the same location as recommended by Lear and Sandeman (1980). Scale annuli were discerned by standard criteria (Havey 1959; Berg and Grimaldi 1967); distances were measured from the focus along the longest oral radius (Tesch 1968). The areas on the scale chosen for analysis were similar to those used by Lear and Misra (1978). We thought they would best reflect differences in growth in both marine and freshwater environments between salmon of North River origin and those from other rivers. As well, because measurements of scale radii appear to be well correlated to length of Atlantic salmon (Kerr 1961; Jones 1949), they were logical selections for scale characters to use in separating North River origin salmon from those fish of other rivers in St. Ann's Harbour. The four characters used were (1) longest oral radius of the 1st yr spent in freshwater (WR1), (2) longest oral radius of the 2nd yr spent in freshwater (WR2), (3) longest oral radius of the 3rd yr spent in freshwater (WR3), and (4) longest oral radius of the 1st yr spent in the sea (WS1).

Theoretical Considerations

The nature of the problem suggested to us the appropriateness of multivariate statistical procedures which recognize the interdependence of variables and provide a single composite of these, determined in some optimal way. These approaches contrast with the use of several univariate statistical analyses carried out separately for each variable that would ignore correlations among variables (Bliss 1970; Kshirsagar 1972). Because we are attempting to determine if unknown individuals, considered singly, belong to a given population, we are not attempting to discriminate between two or more populations. At the univariate level, Sokal and Rohlf (1969, Section 9.5) considered this problem as a special case of comparing two samples and recommended Student's *t*-test to examine "whether or not a single specimen sampled at random could belong to a given population." The individual of unknown origin was regarded as a sample, of size 1, and the difference between the means of this sample and a sample from the population were tested by Student's *t*-test. R. K. Misra extended this methodology to the multivariate level and wrote the computer program (in Fortran IV and supported by an IBM/370 computer). The multivariate methodology, developed primarily from Morrison (1976), is explained as follows.

Let random samples of N_i, $i = 1, 2$, observations on a $p (= 4)$ dimensional variate $\underline{Y}_i$ be drawn from two multivariate normal populations with the same, though unknown, covariance matrix of full rank p.

Let $\underline{\bar{y}}_1$ and $\underline{\bar{y}}_2$ be the row vectors of means of the two samples and S the estimate of the common covariance matrix, so that, for four character variables as in our study,

$$\underline{\bar{y}}_i = \bar{y}_{i1}, \ldots, \bar{y}_{i4}.$$

Hotelling's T^2 is then (Morrison 1976, p. 137)

$$(1)\quad T^2 = \frac{(N_1 N_2)}{N_1 + N_2} (\underline{\bar{y}}_1 - \underline{\bar{y}}_2) S^{-1} (\underline{\bar{y}}_1 - \underline{\bar{y}}_2)'$$

where prime denotes transposed form of the vector. This may be expressed as

$$(2)\quad \frac{N_1 N_2}{N_1 + N_2} \underline{d} S^{-1} \underline{d}'$$

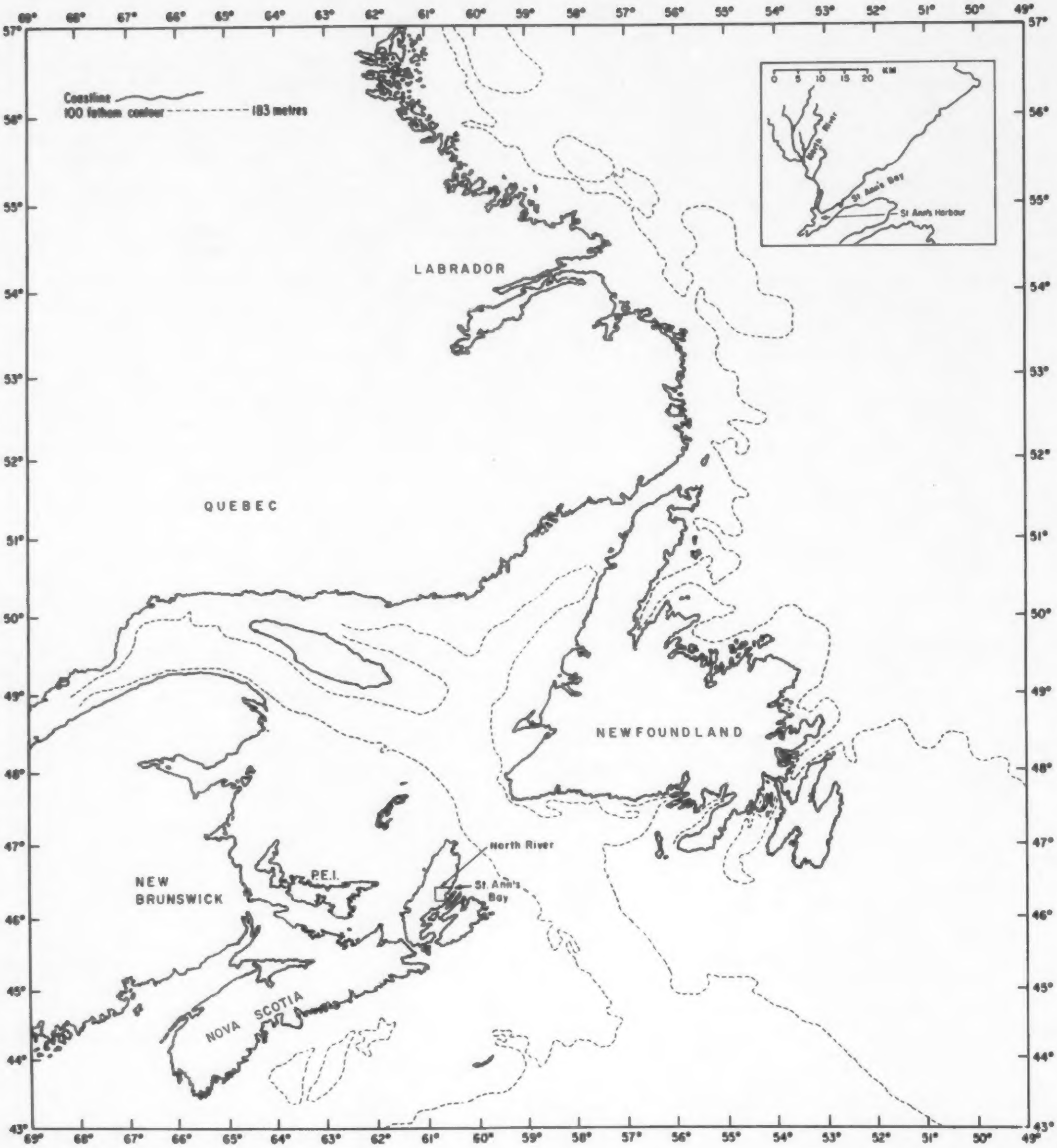
Coastline
100 fathom contour
183 metres
0 5 10 15 20 KM
North River
St. Ann's Bay
St Ann's Harbour
LABRADOR
QUEBEC
NEWFOUNDLAND
NEW BRUNSWICK
P.E.I.
NOVA SCOTIA
North River
St. Ann's Bay
69° 68° 67° 66° 65° 64° 63° 62° 61° 60° 59° 58° 57° 56° 55° 54° 53° 52° 51° 50° 49°
57° 56° 55° 54° 53° 52° 51° 50° 49° 48° 47° 46° 45° 44° 43°

FIG. 1. Location of St. Ann's Harbour and North River from which commercial and sport samples of Atlantic salmon were taken for analysis by Hotelling's T^2 statistic.

where $\underline{d}$ is the row vector of differences in means of individual characters, i.e. $\bar{y}_{11} - \bar{y}_{21}, \bar{y}_{12} - \bar{y}_{22}, \bar{y}_{13} - \bar{y}_{23}, \bar{y}_{14} - \bar{y}_{24}$. The degrees of freedom (df) associated with this statistic are $p(= 4)$ and $N_1 + N_2 - 2$ (Timm 1975). As Morrison (1976) has pointed out, this statistic is derived by application of the union-intersection or likelihood-ratio principles. The F-statistic associated with Hotelling's T^2 is

$$F = \left[\frac{N_1 + N_2 - p - 1}{(N_1 + N_2 - 2)p}\right] T^2$$

and has the variance ratio F distribution with df $= p$ and $(N_1 + N_2 - p - 1)$ (Morrison 1976). The following are noted. (1) The expression $\underline{d}S^{-1}\underline{d}'$ is known as Mahalanobis distance, D^2, of two multinormal populations (Morrison 1976, p. 235). Hotelling's T^2 is proportional to D^2, with $N_1 N_2/(N_1 + N_2)$ being a constant. (2) Mahalanobis distance has been employed to estimate the distance of one single unknown individual (observation) from the mean of a population (Morrison 1976, p. 241, expression 5). Obviously, since the only difference between Hotelling's T^2 and Mahalanobis distance is the proportionality factor, the null hypothesis H_0: $\underline{\mu}_1 = \underline{\mu}_2$ (Morrison 1976, p. 137), where $\underline{\mu}_1$ is a vector of observations on one single individual and $\underline{\mu}_2$ is the vector of means of a population, can be tested by Hotelling's T^2. We have assumed that the two samples were drawn from multinormal populations with a common covariance matrix. The assumption, as with discriminant analysis, of equal covariance matrices is an important one. However, in this case any testing of this assumption is not feasible, as we are comparing from the commercial fishery sample an individual (sample size = 1) drawn from this unknown population with the sample of known origin from North River ($N = 48$). Since there are 29 individuals in the commercial sample, this is repeated 29 times. Therefore, at any one time, the unknown sample consists of only one individual for which it is impossible to derive a covariance matrix. Another good reason for choosing T^2 is because of its properties of invariance and independence of the unknown covariance matrix. The similarity of the two-sample T^2 and discriminant function (Morrison 1976, Section 6.2) is shown as follows.

The linear discriminant function is

$$(3) \quad \underline{d}S^{-1}\underline{y}'$$

where $\underline{d}S^{-1}$ is as in (2). Therefore, the difference in mean discriminant scores for two samples is $\underline{d}S^{-1}(\bar{y}_{11} - \bar{y}_{21}) + \ldots + \underline{d}S^{-1}(\bar{y}_{14} - \bar{y}_{24})$ or $\underline{d}S^{-1}\underline{d}'$ of (2). However, discriminant functions are employed "to summarize observations from the groups on a one-dimensional scale that *discriminates* between the populations" as opposed to testing "the usual hypothesis of equal mean vectors" (Morrison 1976, p. 231). We decided therefore to address the task in hand on the basis of Hotelling's T^2 procedure rather than that of a discriminant function.

The generalized distance function, $\underline{d}S^{-1}\underline{d}'$, has been suggested as a method for classifying individuals into populations (Cooley and Lohnes 1971). The expression for χ_{ji}^2 of Cooley and Lohnes (1971) is the same as $\underline{d}S^{-1}\underline{d}'$ of (2) when (i) one of the two samples consists of only one individual and (ii) the covariance matrix of the population from which the other sample was derived is known or is estimated from a large sample, perhaps in excess of 100 observations (Morrison 1976, p. 164). When the covariance matrix is known, the resulting T^2 is referred to as chi-square (Harris 1975). Therefore we are using essentially the same procedure as suggested in Cooley and Lohnes (1971) except that we employ T^2 instead of chi-square because our sample size is less than 100.

Hotelling's T^2 statistic was estimated for the difference between the vector of the four measurements of an unknown individual and the corresponding mean vector of the sample from the known stock. One individual at a time was analyzed employing the error covariance matrix based on "within sample" variations pooled over two samples, which in the present case is the same as the within sample covariance matrix. T^2 values, with df = 4 and 47, and associated F-values with df = 4 and 44 were then calculated and compared with their corresponding critical values for significance.

Lachenbruch (1967) and Kshirsagar (1972) showed that one could obtain almost unbiased confidence intervals for the probability of misclassification for a given discriminant function using the observations from which it is computed. This "leave-one-out" procedure is similar to the "jackknife" technique (Quenouille 1956; Tukey 1958). The generalization to our method was inherent, as this method of estimating misclassifications is independent of the statistical technique used. This leave-one-out procedure entails carrying out an analysis on individuals by removing the first individual and then comparing this individual to the other $N - 1$ individuals using T^2 with df = 4 and 46 and associated F on df = 4 and 43. This is repeated for all individuals, each time removing one of the individuals and then comparing it with all the others.

Results

We used Hotelling's T^2 (and its associated F-statistic) to test the overall null hypothesis that the sport and commercial fish populations did not differ with respect to the means on any of the four measurements (Table 1). An estimate of T^2 (13.29) with df = 4 and 75 was significant ($P < 0.05$) and the null hypothesis was, therefore, rejected. The T^2 procedure was then extended to test the significance of the difference between four scale measurements of each individual fish of the commercial sample and the respective means of the sample from the angling catch. Six (out of 29) associated F-values were significant (at $P < 0.05$ for two individuals and $P < 0.01$ for four individuals), indicating that 23 of the 29 fish or 79% of the sample of fish caught commercially in St. Ann's Harbour originated from North River. The origin of the other six fish (21%) of the sample remains unknown.

The rate of misclassification using the leave-one-out technique was 4 out of 48 or 8% of the known sample from the angling catch. This suggests that 8% of the unknown commercial sample that was identified as originating from North River was misclassified and that these fish may not in fact have originated from North River. This error rate was considered acceptable. If all 29 fish in the unknown commercial sample had originated in North River, T^2 would have misidentified approximately 2.42 fish, and as many as 88% of the sample would have been said to have come from North River.

On the other hand, this method does not tell us the number of fish in the unknown commercial sample identified incorrectly as North River fish that belonged to some other population. We had this in mind when the 5% level was chosen for significance because four out of the six fish that were significantly different had probabilities less than 1%, which suggests that the magnitude of the problem is small. The Roy–Bose simultaneous confidence intervals (Morrison 1976) with confidence coefficient of 0.95 computed for the means of individual characters

TABLE 1. Statistics of scale characters used for analysis from the angling fishery (sample size = 48) on North River, Nova Scotia, and commercial fishery (sample size = 29) in St. Ann's Harbour, from 1978 catches of Atlantic salmon. The measurements were of the longest oral radius of WR1, first river year; WR2, second river year; WR3, third river year; and WS1, first sea year.

Variable	Mean (mm)	SE
North River angling fishery		
WR1	31.0	0.89
WR2	30.6	1.06
WR3	25.5	0.92
WS1	181.5	2.72
St. Ann's Harbour commercial fishery		
WR1	25.4	1.97
WR2	25.0	2.03
WR3	20.3	1.78
WS1	161.1	11.00

are as follows: WR1, 28.06–33.98; WR2, 27.07–34.10; WR3, 22.47–28.57; WS1, 172.51–190.58. The extent of the misclassification problem will depend on the fraction of stocks with means within these ranges. Some fish that come from populations with means within these ranges may be identified incorrectly as North River fish. More extensive examination of this problem would depend on the choice of the noncentrality parameter and the power of Hotelling's T^2 test (Kshirsagar 1972).

Discussion

We have considered the situation where scale samples from fish of known origin were available from only one of the stocks contributing to a mixed-stock fishery. This is an important approach to the problem of stock identification, as usually it is impossible to obtain samples from all stocks contributing to a particular fishery; often we may not know which stocks are involved. For this situation, discriminant analysis is quite inappropriate; but it is important that we determine the proportion of fish from specific river stocks which are harvested in various mixed-stock fisheries. The most appropriate statistical technique, considering the available sample sizes and assumptions of the model, was Student's *t*-test (Sokal and Rohlf 1969) at the univariate level and Hotelling's T^2 (Morrison 1976) at the multivariate level.

The choice of variables is also important. They must be chosen to exploit differences among growth characteristics of stocks that arise from temporal and/or spatial separation of stocks caused by differences in life-history strategies. Thus, the variables have been chosen from both freshwater and marine phases of the salmon life history. The fact that samples from angled and commercial fish populations differed significantly indicates that these variables are adequate for stock identification.

The number of variables chosen for analysis is also important. Other studies (Bliss 1970; Lachenbruch 1975) have demonstrated that four variables, especially in discriminant analysis, are sufficient on which to draw conclusions. Bliss (1970) compared the calculation of a discriminant function with that of multiple regression but with x and y reversed. In a multiple regression analysis, the expected value of R^2 (the multiple correlation coefficient) is equal to $K/N - 1$ (Morrison 1976) where K is the number of variables in a sample of size N. Hence, as K increases, so does R^2, even if there is in fact no correlation between x and y, so that any seemingly successful discrimination based on a large number of variables may be no more than just an artificial inflation of its discriminatory power caused by choosing an unduly large number of variables. This would apply equally well to T^2 (because discriminant function is related to the two-sample Hotelling's T^2, as already pointed out).

A number of methods have been used to determine the river of origin of salmon stocks caught in mixed-stock fisheries. Tags applied to fish in the adult or smolt stage is one of the simplest and more reliable methods. Tags applied to salmon smolts have shown that salmon caught in the Newfoundland commercial fishery originated from rivers in Labrador, Newfoundland, Quebec, New Brunswick, and Nova Scotia (Murray 1966; Elson 1971; Kerswill 1971; Pratt et al. 1974). However, nonreporting of recaptures, high numbers of tagging mortalities, and subsequent low overall numbers of returns (Ireland and Kanwisher 1978) make derivation of total catches of single stocks using tag recaptures unreliable.

Other techniques based on biological characteristics of stocks have been examined for their efficiency in stock separation. For example, Pippy (1969) could not differentiate between Canadian Atlantic salmon stocks when using parasites as biological tags. Others using serum electrophoresis have attempted stock discrimination on the basis of gene frequencies coding for various tissue proteins and enzymes (Nyman 1967; Møller 1970; Payne et al. 1971; Nyman and Pippy 1972; Wilkins 1972; Payne 1974) but without much success, as shown by Fairbairn (1979). Another disadvantage of these techniques is that they could not distinguish stock identity for each individual fish in a sample, as only an overall proportion could be derived based on the allele frequencies.

Wider use has been made of morphological characters of fishes to identify stock components in mixed-stock fisheries. Morphological characters have been analyzed by discriminant analysis to identify continent of origin of Pacific salmon (Fukuhara et al. 1962; Dark and Landrum 1964). Scale characters have been incorporated into a linear discriminant function that has been used to separate chum and sockeye salmon from mixed-stock fisheries in the Pacific Ocean into populations of Asian and North American salmon (Anas and Murai 1969; Tanaka et al. 1969). Lear and Sandeman (1980) successfully used meristic scale characteristics to identify European and North American populations of Atlantic salmon in the West Greenland area. Lear and Misra (1978) employed a discriminant function to identify a geographic clinal trend in scale characters of stocks of Atlantic salmon along the Atlantic coast of North America.

Recently, Cook and Lord (1978) have proposed a polynomial discriminant method for the racial classification of stocks of sockeye salmon. This method utilized scale characters and a priori probability estimates to identify Bristol Bay, Alaska sockeye salmon in an unknown sample taken on the high seas south of the central Aleutian Islands. The use of this technique to separate racial stocks of Atlantic salmon has two significant drawbacks: (1) the unknown specimen or unknown specimens must genuinely belong to one of the populations from which the known sample or known samples originated (Reyment 1966) and (2) the method is not very robust relative to the a priori probabilities used (Corruccini 1975).

These techniques of scale-pattern recognition have been used on both coasts of North America (Atlantic, Lear and Misra 1978 and Lear and Sandeman 1980; Pacific, Cook and Lord 1978 and Cook 1982) for stock identification because of their advantages over other morphological characters. Scales are easily obtained from fish of known stock origin in their home rivers either from the angling fisheries or at counting-fence facilities; other anatomical features are difficult, if not impossible, to obtain because they require that the fish are killed and returned for later laboratory study. As well, the large numbers of specimens required often preclude the use of anatomical structures of fish in small rivers where a significant proportion of the run to the river may be required for analysis.

Techniques other than tagging are required because of the expense and infrequent recaptures of tagged fish. Whereas the technique we presented tells us the proportion of the catch that is of local origin, it reveals nothing about the proportionate composition of the more distant stocks. The usefulness of Hotelling's T^2 is shown when samples from all the rivers of origin are unknown, thereby precluding the use of discriminant analysis.

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Work Satisfaction and Community Attachment among Fishermen in Southwest Nova Scotia

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Social scientists have examined the problem of attachment to the New England fisheries in terms of two interacting influences: work satisfaction, based on questionnaire interviews, and attachment to kin and community, based on ethnographic field research. There is a paucity of equivalent information for the Maritimes. This study replicates the New England work satisfaction studies, and includes additional questions concerning community attachment. We demonstrate that fishermen in southwest Nova Scotia are, in contrast with their New England counterparts, satisfied with *all* questions about their work (save for the common dissatisfaction with government officials found in both the Nova Scotia and New England samples). In particular, although offshore fishermen in southwest Nova Scotia tend to be somewhat less satisfied than those who fish inshore or both inshore and offshore, they have, by comparison with the New Bedford fishermen, scores that are over the "neutral value" on all time and adventure questions. The underlying factors of job satisfaction are comparable with those in the New England studies, except that the factors in our data are more numerous and simpler to interpret. High job satisfaction is combined with strong community attachments in southwest Nova Scotia.

En Nouvelle-Angleterre, des experts en sciences humaines ont étudié le problème de l'attachement à la pêche sur le plan de deux influences à action réciproque : la satisfaction au travail évaluée à l'aide de questionnaires et l'attachement aux parents et à la collectivité d'après des recherches ethnographiques sur le terrain. Il existe peu de données du genre pour ce qui est des provinces Maritimes. La présente étude reprend celles menées sur la satisfaction au travail en Nouvelle-Angleterre et comprend des questions supplémentaires sur l'attachement à la collectivité. Les auteurs montrent que les pêcheurs du sud-ouest de la Nouvelle-Écosse, au contraire de leurs confrères de la Nouvelle-Angleterre, sont satisfaits sur *tous* les aspects de leur travail (sauf pour ce qui est de l'insatisfaction envers les fonctionnaires gouvernementaux, qui est commune aux deux groupes). En particulier, les pêcheurs hauturiers du sud-ouest de la Nouvelle-Écosse semblent moins satisfaits que les pêcheurs côtiers ou ceux qui pêchent dans les deux zones, mais ils ont obtenu des notes supérieures à la valeur neutre pour toutes les questions relatives au temps et à l'aventure par rapport aux pêcheurs de New Bedford. Les facteurs dont dépend la satisfaction au travail sont comparables à ceux retrouvés dans l'étude menée en Nouvelle-Angleterre sauf qu'ils sont moins nombreux et plus simples à interpréter. Dans le sud-ouest de la Nouvelle-Écosse, une satisfaction élevée au travail est combinée à un attachement prononcé à la collectivité.

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Dramatic changes have recently occurred in the manner in which the marine environment and its coastal zone have been treated. Nowhere is this more the case than along the east coast of the United States and Canada. Developments such as the declaration of a 200-mi fishing zone and the push for offshore exploration and development of hydrocarbons have had ramifications within social and economic spheres which promise to be far-reaching and long-lasting. The coastal communities, established for fishing and maritime commerce and still dependent on the sea, will bear the main impact of any changes in resource access, employment, and of various development activities. Thus, it is essential to understand how inhabitants perceive their present-day existence. Do they enjoy work as fishermen? If so, which components of work satisfaction are most significant to them? Many rural communities have been in existence for more than 200 yr. Do people continue to live in these small villages by choice, or from lack of alternatives? Is work satisfaction a prime reason for wishing to remain within the community, or is the work secondary to other factors related to place?

Questions such as these have rarely been studied for fishing communities despite recognition of their distinctive economies (Firth 1975; Acheson 1981) and the generally expressed desire for an improved understanding of fishing as an occupation (Anderson 1978). Within Canada the best studied communities are in Newfoundland (Brox 1972; Faris 1966; Firestone 1967), especially those inaccessible by road. However, Newfoundland outport communities bear limited resemblance to communities elsewhere along the east coast. In particular, the communities of southwest Nova Scotia require attention, as this area contains the greatest concentration of coastal villages in the Maritime provinces of Canada. These communities face an immediate threat of potential reduction in access to fisheries on Georges Bank as a consequence of the Gulf of Maine boundary and

TABLE 1. Interview completions.

	County					
	Lunenburg	Queens	Shelburne	Yarmouth	Digby	Total
Interviews completed	126	48	197	136	89	597
Potential interviews	181	54	237	158	120	750
No longer fishing	20	4	12	20	11	67
Completion rate as a percentage of those fishing	78.3	96.0	87.6	98.6	81.7	87.4

fisheries dispute between the United States and Canada (Wang 1981).

The fishing communities of southwest Nova Scotia have three distinctive origins: French settlers from the seventeenth century, New England fishermen and Loyalist settlers in the eighteenth century, and German settlers to Lunenburg from 1751. Many of the communities retain ethnic characteristics associated with their origins. Furthermore, there are distinctive fishermen groupings either within or between communities based on the type of fishing: inshore and offshore, scallopers, herring, ground fishermen, draggers, and longliners. All of these characteristics and groupings might be expected to influence job satisfaction and possibly attachment to community.

Within the Gulf of Maine region, the most detailed studies on work satisfaction and community attachment are those of New England ports (Point Judith, Rhode Island; New Bedford, Massachusetts; and the Pemaquic Peninsula in Maine) by Poggie and Pollnac (1978) and Pollnac and Poggie (1979). These studies are based on interviews with fishermen. They attempt to achieve an understanding of relative satisfaction with fishing as a way of life and how port-by-port situations may influence this satisfaction.

The aim of the present study is to survey fishermen in southwest Nova Scotia in a fashion parallel to the New England studies in order to establish levels of work satisfaction and community attachment. It is hypothesized that the fewer alternative employment opportunities and the long-standing stability of kinship within small villages of southwest Nova Scotia make this region, compared with the New England ports, a distinctive fourth population characterized by a strong attachment to the fishery, high work satisfaction, and strong ties to kin and community.

Methods

Our study replicated the job satisfaction questions employed by Poggie and Pollnac (1978, p. 233–235) and Pollnac and Poggie (1979, p. 3–6) and added some further questions on work conditions and community attachments which are relevant to this topic. We have identical or very similar question formats for all the background characteristics used in the American studies, save for ethnicity. They define ethnicity as being "born inside or outside the United States" (Poggie and Pollnac 1978, p. 235), while we have employed "the first language you spoke which you still understand: French/other/English." We also have included several additional relevant demographic and work-specific questions.

The analysis for southwest Nova Scotia presented in this report is based on 597 interviews completed with a stratified random sample of 683 possible respondents in the five western counties of Nova Scotia during October–December 1982. This sample covers all fishing communities from Northwest Cove in Lunenburg County along the coast to Westport on the southern tip of Digby Neck. The initial stratified random sample consists of 750 names from a list of 5197 current fishing license holders in the five western counties of Nova Scotia (the sample was provided by the Department of Fisheries and Oceans). As indicated in Table 1, the population of 5197 was separated by county, and a 14.4% random sample was taken from each county.

The fieldwork was conducted between October 23 and December 9, 1982, by 37 trained interviewers located in or near the various fishing communities. The fact that almost all of the interviewers had previous experience working for Statistics Canada on labour force surveys or the federal government census meant that they were already familiar with similar questions, and that they were able to conduct their interviews over a relatively short period. This experience also helped produce good quality data which required few phone-backs and little cleaning. Both possible-punch and contingency checks were conducted in data cleaning.

As indicated in Table 1, the overall completion rate for the survey, after those who report they are no longer fishing are excluded, was 87.4%. Given current survey standards, this figure indicates a high level of success. One minor bias suggested by the data, and confirmed by discussions with the interviewers, is that somewhat lower return rates for Lunenburg and Digby counties are attributable to our inability to contact or interview some offshore fishermen there during the relatively short fieldwork period.

Results and Discussion

Distribution of and Factors Underlying Work Satisfaction

The New England studies contain little descriptive information on the actual distribution of their respondents on specific job attitudes. They do indicate that the 79 respondents in the Point Judith, Rhode Island, sample are above the mean on all 26 job attitude questions (see Table 2 for a list of the questions) except one concerning the performance of federal and state (provincial) officials, and that the 42 respondents in the New Bedford, Massachusetts, sample are below the mean on five questions about time (questions h, j, m, t, and z in Table 2) and one about adventure (question n in Table 2), as well as the one regarding state and federal officials (Poggie and Pollnac 1978, p. 239). They also state that the means on a question concerning the ability to be one's own boss (item u in Table 2) are 4.3 and 3.5 for Point Judith and New Bedford, respectively (Poggie and Pollnac 1978, p. 250).

Given that the Point Judith fishermen predominantly work on smaller vessels for short trips (less than 4 d), and that the New Bedford fishermen are primarily working on large offshore

TABLE 2. Mean score[a] on the work satisfaction questions by inshore and/or offshore status[b] (possible response range = 1–5).

Question	Inshore and/or offshore status				Significance level[c]
	Inshore	Both	Offshore	All	
(l) Performance of federal and provincial officials	2.47	2.22	2.25	2.36	NS
(g) Regular income	3.15	3.26	3.37	3.23	NS
(o) Your earnings	3.25	3.41	3.42	3.33	*
(e) Crowding	3.50	3.05	3.52	3.38	***
(a) Physical fatigue	3.73	3.54	3.28	3.58	**
(c) Mental pressure	3.73	3.46	3.52	3.61	NS
(j) Time for family activities and recreation	3.94	3.49	3.32	3.68	***
(r) Job safety	3.84	3.83	3.50	3.76	*
(h) Hours spent working	3.92	3.67	3.52	3.77	NS
(t) Time away from home	4.10	3.55	3.33	3.79	***
(m) Time it takes to get to the fishing grounds	4.15	3.65	3.89	3.96	***
(v) Peace of mind	4.18	3.97	3.54	3.98	***
(s) Living conditions on board	3.94	4.06	4.06	4.00	***
(k) Doing deck work on vessel	3.99	4.13	3.93	4.02	*
(x) Cleanliness	4.16	4.06	3.76	4.05	***
(n) Adventure	4.22	4.14	3.92	4.13	NS
(z) Trip length	4.37	3.96	3.80	4.14	***
(f) Challenge	4.24	4.28	4.15	4.23	NS
(u) Opportunity to be your own boss	4.53	4.31	3.68	4.29	***
(q) Ability to come and go as you please	4.53	4.37	3.68	4.30	***
(d) Healthfulness	4.46	4.37	4.04	4.35	**
(w) Feeling you are doing something worthwhile	4.43	4.42	4.17	4.37	***
(p) Being out on the water	4.54	4.47	4.09	4.43	***
(b) Fellow workers	4.43	4.49	4.42	4.45	NS
(i) Community in which you live	4.60	4.47	4.50	4.54	NS
(y) Working outdoors	4.81	4.80	4.52	4.75	***
Number of respondents	302	167	126	597	

[a] Answer categories for each are (1) "very dissatisfied," (2) "moderately dissatisfied," (3) "neutral," (4) "moderately satisfied," and (5) "very satisfied."

[b] Respondents were asked "5.b. Where do you fish most of the time?," with the answer categories being "inshore," "offshore," or "both."

[c] These significance levels represent the Chi-square values for the cross-tabulations of the inshore and/or offshore status by the respective job satisfaction items. For example, this means that the cross-tabulation of inshore and/or offshore status by physical fatigue is significant at the 0.01 level. *Significant at the 0.05 level; **significant at the 0.01 level; ***significant at the 0.001 level; NS, not significant at the 0.05 level.

draggers for long trips (4 d or more) (Pollnac and Poggie 1979, p. 3), we have divided our sample in Table 2 into three self-designated groups according to whether they report fishing inshore, offshore, or both. However, as may be observed in Table 2, our respondents in southwest Nova Scotia, regardless of their fishing status, uniformly score over the "neutral" value of 3 on all work attitude questions except the one on government officials. Although there is a tendency for those in the offshore fishery to be somewhat less satisfied than others, they do, in contrast with the New Bedford fishermen, score over the mean on all time and adventure questions. Also, it may be noted that those who mainly fish inshore, or a combination of inshore and offshore, have a somewhat higher mean score (4.53 and 4.31, respectively) on the "opportunity to be your own boss" question than their counterparts in Point Judith, and that our offshore fishermen have a higher mean (3.68) than the New Bedford fishermen. Similar patterns are obtained if one divides our sample in terms of trip length, rather than inshore and offshore.

To simplify our understanding of the job satisfaction questions, we have done a factor analysis of the 26 questions to try to identify common factors among them. Factor analysis is a statistical technique which permits us to detect the existence of underlying factors among our questions and allows us to determine the relative strength of each question's connection with that factor.

Poggie and Pollnac (1978, p. 235–239) reported four factors among the work questions for the Point Judith fishermen: "time," "outdoors," "earnings," and "independence." In addition to these four factors, their factor analysis for New Bedford also identified an "offshore" factor, and a "work quality" factor. When they merged the Rhode Island and Massachusetts interviews with the ones from Maine (for a total of 201 respondents), the basic factors were reduced to three: "time," "earnings," and "adventure" (Pollnac and Poggie 1979, p. 4–6).

The basic factors underlying the work attitude questions for southwest Nova Scotia were comparable with those found for the New England fishermen, save that ours (Table 3) are more numerous and somewhat easier to interpret. The factors are inductively defined by the social investigator in terms of the questions which have the highest "loadings" on the particular factor (a loading measures the extent to which questions are involved in particular factor patterns). As Rummel (1967, p. 463) put it, loadings "can be interpreted *like correlation coefficients* — the square of the loading multiplied by 100

TABLE 3. Factor analysis of the work satisfaction questions (varimax rotation).

Question	Factor							
	Independence	Work quality	Earnings	Time/trip length	Adventure	Offshore	Time/family	Crowding
(a) Physical fatigue	0.10889	0.52257	0.07740	0.09431	0.10536	0.13155	0.16260	0.07134
(b) Fellow workers	0.02930	0.17580	0.07488	0.35161	0.10648	0.13894	0.06441	−0.02510
(c) Mental pressure	0.02817	0.65510	0.08608	0.15793	0.01991	−0.02777	0.01049	0.23136
(d) Healthfulness	0.31605	0.39586	0.07318	0.11180	0.08358	0.12825	0.06490	0.05706
(e) Crowding	−0.13649	0.27372	−0.00922	0.15913	0.06421	0.10009	0.07967	0.46443
(f) Challenge	0.11240	0.10346	0.05790	0.18625	0.53665	0.09193	−0.02160	0.09318
(g) Regular income	−0.04116	0.12349	0.90222	0.02214	0.03947	0.09611	0.06672	0.03582
(h) Hours spent working	0.24061	0.29418	0.21534	0.14082	0.22552	0.09151	0.44649	0.10221
(i) Community in which you live	0.08283	0.14705	0.05975	0.23671	0.14030	0.03739	0.06419	0.08418
(j) Time for family activities and recreation	0.28253	0.22761	0.07183	0.22108	0.03200	0.08549	0.45572	0.08379
(k) Doing deck work on vessel	0.03824	0.31725	0.03909	0.26958	0.16569	0.23624	0.17250	−0.24641
(l) Performance of federal and provincial officials	0.08572	0.08720	0.14938	0.01910	0.01288	0.02890	0.04187	0.31352
(m) Time it takes to get to the fishing grounds	0.01421	0.07013	−0.00154	0.33719	0.22178	0.16004	0.22622	0.23869
(n) Adventure	0.22499	0.07583	0.00093	0.09396	0.72974	0.10892	0.17599	−0.02918
(o) Your earnings	0.01201	0.06609	0.81685	0.07080	0.04088	0.06663	0.04476	0.13013
(p) Being out on the water	0.45008	0.12727	0.01485	0.16726	0.06639	0.15641	0.04300	0.02758
(q) Ability to come and go as you please	0.70815	0.08228	−0.03603	0.04051	0.10475	0.08755	0.21531	−0.02263
(r) Job safety	0.23251	0.35332	0.04747	−0.01687	0.08953	0.38699	0.11636	0.20793
(s) Living conditions on board	0.06065	0.05064	0.08514	0.17891	0.12648	0.58668	0.12242	−0.01012
(t) Time away from home	0.39825	0.11119	0.03647	0.40171	0.03232	0.18756	0.45200	0.21294
(u) Opportunity to be your own boss	0.66405	0.01978	−0.02170	0.04204	0.11299	0.03476	0.09950	0.01674
(v) Peace of mind	0.38063	0.38179	0.02237	0.03264	0.15475	0.14357	0.11891	0.32070
(w) Feeling you are doing something worthwhile	0.40116	0.19028	0.14970	0.22305	0.31022	0.20019	−0.04434	0.12423
(x) Cleanliness	0.25729	0.12966	0.08375	0.19567	0.07429	0.57681	−0.02231	0.15354
(y) Working outdoors	0.36653	0.06727	−0.01578	0.36681	0.23461	0.01498	−0.10586	−0.10210
(z) Trip length	0.26509	0.03311	−0.01158	0.55112	0.05686	0.20296	0.20013	0.18559
Eigenvalues	5.57	1.67	0.98	0.81	0.68	0.55	0.44	0.37

equals the percent variation that a variable has in common" with a factor (emphasis his). For example, the first factor in our data, "independence," is primarily defined by questions q, u, p, and w, with factor loadings for the four questions being 0.70815, 0.66405, 0.45008, and 0.40016. Our factors are ordered from left to right in terms of the percent of variation among all variables involved in the factor analysis (their "eigenvalues"). Although this ordering is sometimes regarded as an estimate of the relative importance, one must be cautious about such a simple view, as variations in eigenvalues may merely reflect a difference in the number of *potential* questions which measure a particular factor. Such an imbalance in the number of questions may well explain why the "independence" factor has appeared first, as it has at least four questions loading on at the 0.4 level.

As shown in Table 3, we found that there are eight factors underlying the work attitude questions: five of the six factors identified above for New Bedford, the sixth New Bedford factor (time) split into two factors (trip length and time for family), and an additional factor not present in the New England studies (crowding). In Table 4, we have, for purposes of comparability, listed all questions in the various samples which are related to the particular work attitude factor at the 0.4 level or above (a conventional lower boundary in factor analysis for important associations). As may be observed in this table, 13 of the 18 questions which are important in interpreting the eight factors in our study also appear on the same factor in the New England data.

After having identified our major work satisfaction factors, we constructed some work attitude indices as summed measures of the major questions which define the factors. Scale analysis was undertaken to eliminate weak or redundant questions. Table 5 provides a list of the indices, the component questions, and their respective Cronbach's alpha values.

Table 6 presents the correlations among the work attitude indices and some overall work satisfaction questions. Poggie and Pollnac used the second and third questions in Table 4 concerning whether or not one would go into fishing if one had one's life to live over, and whether or not one would advise a young man to go into fishing as indicators of overall work satisfaction (Pollnac and Poggie 1979, p. 6–9). They found that the three factors (time, earnings, and adventure) they isolated for their total sample were all significantly related to the second question, but that only the earnings factor was a significant correlate of whether or not one would advise a young man to

TABLE 4. Questions defining the work satisfaction factors in the Nova Scotia and New England samples.[a]

	Sample			
Factor	Southwest Nova Scotia		All New England fishermen[b]	
Independence	Ability to come and go as you please	0.72		
	Opportunity to be your own boss	0.66		
	Being out on the water	0.45		
	Feeling as if you are doing something worthwhile	0.40		
Work quality	Mental pressure	0.66		
	Physical fatigue	0.52		
	Healthfulness	0.40		
Earnings	Regular income	0.90	Cleanliness	0.59
	Your earnings	0.82	Physical fatigue	0.56
			Regular income	0.49
			Mental pressure	0.48
			Job safety	0.45
Time/trip length	Trip length	0.55	Time away from home	0.81
	Time away from home	0.40	Hours spent working	0.72
			Time for family activities and recreation	0.71
			Ability to come and go as you please	0.61
			Time it takes to get to fishing grounds	0.47
			Doing deck work on vessel	0.41

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mples.[a]

	Sample			
	Point Judith, Rhode Island		New Bedford, Massachusetts	
	Ability to come and go as you please	−0.68	Opportunity to be your own boss	0.84
	Performance of federal and state officials	−0.68	Challenge	0.58
	Opportunity to be your own boss	−0.65	Community in which you live	0.42
			Physical fatigue	−0.71
			Mental pressure	0.63
			Performance of federal and state officials	0.63
			Regular income	−0.52
			Community in which you live	−0.44
9	Your earnings	0.68	Your earnings	0.77
6	Fellow workers	0.68	Ability to come and go as you please	−0.70
9	Regular income	0.54	Job safety	0.60
8	Mental pressure	0.49	Fellow workers	0.57
5	Physical fatigue	0.45		
1	Time away from home	0.85	Time away from home	−0.83
2	Hours spent working	0.61	Trip length	−0.78
	Peace of mind	0.53	Hours spent working	−0.74
1	Time it takes to get to the fishing grounds	0.50	Time for family activities and recreation	−0.68
	Crowding	0.50		
1	Time for family activities and recreation	0.49	Time it takes to get to fishing grounds	−0.63
7	Trip length	0.45	Doing deck work on vessel	−0.54
	Healthfulness	0.42		
1			Feeling you are doing something worthwhile	−0.45

TABLE 4. (*Concluded*).

Factor	Southwest Nova Scotia		All New England fisherme	
Adventure	Adventure	0.73	Being out on the water	−
	Challenge	0.54	Adventure	−
			Challenge	−
			Working outdoors	−
			Feeling you are doing something worthwhile	−
Offshore	Living conditions on board	0.59		
	Cleanliness	0.58		
Time/family	Time for family activities and recreation	0.46		
	Time away from home	0.45		
	Hours spent working	0.45		
Crowding	Crowding	0.46		

[a] Numbers accompanying the questions are "factor loadings," or measures of the extent to whic

[b] "All New England fishermen" includes the 80 Maine interviews. No separate factor analysis o

Sample					
fishermen[b]		Point Judith, Rhode Island		New Bedford, Massachusetts	
		Working outdoors	−0.80	Being out on the	
	−0.71	Being out on the water	−0.77	water	0.77
	−0.71	Adventure	−0.55	Feeling you are doing	
	−0.66	Feeling you are doing		something worthwhile	0.63
	−0.57	something worthwhile	−0.48	Adventure	0.59
g		Challenge	−0.45	Healthfulness	0.42
hile	−0.51	Healthfulness	−0.42	Peace of mind	0.41
				Crowding	−0.93
				Cleanliness	−0.83
				Living conditions	
				on board	−0.63

to which questions are involved in the particular factor.

nalysis of the Maine data has been presented by Poggie and Pollnac.

TABLE 5. Work attitude indices.

Index	Component questions	Cronbach's alpha value[a]
Independence	p, q, u	0.66
Work quality	a, c, d	0.61
Earnings	g, o	0.87
Time/trip length	t, z	0.66
Adventure	f, n	0.62
Offshore	s, x	0.59
Time/family	j, t, h	0.71
Crowding	e	—

[a] Cronbach's alpha is a reliability measure, or an index of the internal consistency of the selected questions. A value of 0.60 is considered acceptable and a value of 0.70 is considered good (Marsh 1977, p. 254–255).

go into fishing. They also discovered that there were more significant connections between their measures of overall work satisfaction and the specific work indices among (1) offshore fishermen as compared with inshore fishermen and (2) fishermen in New Bedford as compared with fishermen in Point Judith and Maine.

As indicated in Table 6, we found only modest or weak correlations between our earnings, time, and adventure indices and the measures of overall job satisfaction used by Poggie and Pollnac. Although there are some stronger connections when one examines our other work indices, particularly independence and work quality, and although most of the associations are statistically significant, they are not very impressive. However, we did find, as in the New England study, that there are stronger and more significant relationships for offshore fishermen.

A few comparative points should be made here. First, the correlations in the overall New England sample are not particularly large, as only two of the six (three factors by two questions) are greater than 0.2 (Pollnac and Poggie 1979, p. 8). Second, the average strength of our associations has been diminished by the greater number of separate factors we have. Our correlations would probably be as high as the New England ones had we arrived at only three, rather than eight, work factors.

In addition, as in the New England data, the work attitude indices are generally more strongly related to the question of going into fishing if one had one's life to live over than they are to advising a young man to go into fishing. We think this occurs because the former question is probably a better summary measure than the latter. We suspect that considerations other than those of personal job satisfaction play a more important role in determining the advice one gives to a young man. At a descriptive level, 82% of our respondents say they would go into fishing if they had to live their lives over, but only 42% said they would advise a young man to go into fishing. Finally, it should be noted that a simple overall satisfaction question about fishing as a job, a question which was not included in the New England study, may well be a better measure than either of the New England measures, since it is related to all eight of the Nova Scotia work factors.

Causes of Work Satisfaction

There are only a limited number of comments that can be made at this time about the causes of work satisfaction. This is true not only because there is relatively little developed theoretical literature relevant to this area, but also because the topic, as shown by the multiplicity of job satisfaction factors, is so inherently complex. Further, the major correlates or predictors of the various work satisfaction factors are so diverse that it is difficult to isolate powerful causal agents.

As shown in Table 7, Poggie and Pollnac were only able to locate recurring variables in their total sample, where "ethnicity," "other than inshore lobstering," and "early entry into fishing" are important determinants of their three work factors (earnings, time, and adventure). Even here, however, their explanations for these predictive relationships are not very convincing. For ethnicity, they argued that the positive connection between ethnicity and earnings in New Bedford "suggests that expectations of foreign born are *lower* that the non-ethnic counterparts" (Poggie and Pollnac 1978, p. 25), *and* that the negative relationships between ethnicity, on the other hand, and time and adventure, on the other, may be a consequence of the fact that "most of the foreign born fishermen in New Bedford are Portuguese immigrants who came to the United States with relatively *high* expectations" (Pollnac and Poggie 1979, p. 40–41) (emphasis ours). Aside from having no persuasive reasons for why expectations should be high in one realm, and low in another, they have no direct empirical evidence on expectation levels.

For early entry into fishing, Pollnac and Poggie (1979, p. 41–42) suggested that the positive relations with the three work factors may reflect either "early socialization to the occupation of fishing" or the lack of "opportunity to compare fishing with other occupations." For "other than inshore lobstermen," they argued (Pollnac and Poggie 1979, p. 42) that predominantly offshore fishermen are more likely to be dissatisfied than inshore lobstermen from Maine with their earnings. Each of these propositions seems plausible enough, but given the lack of supporting evidence, they are far from conclusive.

In our Nova Scotia data, we have been able to locate fewer significant indications of satisfaction with specific work factors, although as shown in Table 7, we do have one significant background characteristic for each of the eight factors. This difference is probably due to the fact that we have more factors to explain using the same statistical criteria. Each of our factors tends to be measured by fewer questions, and is consequently less likely to have as many predictors. This suggestion is consistent with the decline from the total American sample, to Point Judith, and then to New Bedford, in the average number of significant questions per factor (four, three, and two, respectively).

As in the New England data, owner/skipper status is positively related to satisfaction with independence considerations, and early entry into the fishery is positively associated with earnings. The former connection seems rather straightforward, and we might engage in speculation similar to the Americans regarding the importance of early entry for earnings satisfaction. The facts that hours fishing in the average work week predicts work quality and time for the family, that longer length of fishing trip indicates dissatisfaction with the time of trip, or that fishing with a scallop drag predicts dissatisfaction with offshore work require little comment. Fishing with hook and line and lobster traps probably tends to lead to dissatisfaction with crowding because the presence of numerous tubs of lines and lobster traps limits freedom of movement. We have no good hypotheses about the positive connection between fishing for cod and satisfaction with the adventure factor.

TABLE 6. Correlations among work satisfaction indices and overall work satisfaction measures (Pearson product–moment correlations).[a] *Significant at the 0.05 level; **significant at the 0.01 level; ***significant at the 0.001 level.

	Overall work satisfaction measures		
Work satisfaction index[b]	Overall satisfaction with fishing[c]	Live life over: go into fishing[d]	Advise young man to go into fishing[e]
Independence	0.28***	0.33***	0.15***
Work quality	0.13**	0.17***	0.14***
Earnings	0.24***	0.13***	0.08*
Time/trip length	0.13**	0.12**	0.05
Adventure	0.15***	0.06	0.10**
Offshore	0.15***	0.17***	0.08*
Time/family	0.21***	0.17***	0.10**
Crowding	−0.09*	−0.09*	−0.05
Overall satisfaction with fishing	X	0.30***	0.15***
Live life over: go into fishing		X	0.29***
Advise young man to go into fishing			X
	(418)[f]	(597/418)[f]	(597/418)[f]

[a] Pearson product–moment correlations are measures of association which range from −1.00 (perfect negative correlation) to +1.00 (perfect positive correlation). In the context of this study, correlations under ±0.15 are weak, those from ±0.15 to ±0.25 are intermediate, and those over ±0.25 are strong.

[b] There were few missing data or refusals. Of the 26 questions, 21 had less than 15 cases with missing data or refusals, and only 3 were over 30. The maximum value was 68 for question k, a question of concern primarily to offshore fishermen.

[c] The question reads: "17. Overall, how satisfied are you with fishing? The best/one of the best/job(s) you've ever had/above average/average/below average/one of the worst/the worst you've ever had."

[d] The question reads: "18. If you had your life to live over, would you go into fishing? Yes/No."

[e] The question reads: "19. Would you advise a young man who is starting out to go into fishing? Yes/No."

[f] After inspecting the relevant cross-tabulations, missing data and refusals were recoded to the middle score (3) for each question. The number of cases for overall job satisfaction with fishing is lower (418) than that for the other two summary measures (597) because we have included only those who have held more than one job.

Overall Model of Work Satisfaction

In order to focus the discussion on the specific factors and causes of work satisfaction, we will now examine the distribution and major predictors of overall work satisfaction. As shown in Table 8, fishermen in southwest Nova Scotia are considerably more likely than two recent samples of private-sector workers in the Maritimes to regard their current job as the best they have ever had. As compared with 25% of a 1979 general cross-section of private-sector workers in the Maritimes (General Segmentation sample) and 13% of a 1977–78 survey of low-wage workers in the Maritimes (Marginal Work World sample), fully 41% of the fishermen said their job was the best one they had ever had. This pattern demonstrates that fishermen are considerably more satisfied with their jobs, in a summary sense, than workers located in other parts of the Maritime economy.

With regard to the causes of overall satisfaction, we find, as shown in Table 9, that the major determinants include two specific work factors, independence and earnings (standardized partial regression coefficients of 0.23 and 0.21, respectively), as well as religion (−0.22) and part-time/full-time fishing status (0.16). The significant coefficients for the specific work satisfaction indices are in keeping with the general pattern in the job satisfaction literature (M. King, M. Murray, T. Atkinson, Institute for Behavioural Research, York University, Toronto, Ont., unpubl. data) that the major predictors of work satisfaction are work-specific characteristics, as opposed to more general structural consideration, such as social class, rural/urban location, or region. This general pattern makes the moderate coefficient of −0.21 for religion difficult to explain. The negative sign on the coefficient signifies that conservative Protestants are, other things being equal, more likely than Catholics or liberal Protestants to be satisfied with their jobs. The real impetus for this finding comes from the relatively high satisfaction levels among a large group of conservative Protestants (Baptists) in Shelburne County. Field researchers familiar with the area suggest that this may reflect a more general religious and political conservatism which influences their perceptions of the work world. The more liberal views of the Catholic and liberal Protestant respondents may, however, have very different origins.

The positive relationship between full-time fishing license and overall job satisfaction is also interesting, but for a different reason. Although the part-time/full-time variable has very few connections to the specific work items or indices (or to work conditions in general), it nevertheless has a modest negative effect on overall job satisfaction (they still tend to regard their fishing jobs as "average"). Fishermen with part-time licenses tend to be younger, single men who own neither their boats nor their homes. Possibly this type of fisherman may be less satisfied, not from unhappiness with the specific work factors measured in this study, but rather because they are least likely to be able to establish careers in fishing for themselves.

TABLE 7. Significant predictors[a] of the work satisfaction factors in the Nova

Factor	Southwest Nova Scotia		All United States fisherm	
Independence	Owner/skipper	0.51		
Work quality	Hours fishing in average work week	−0.22		
Earnings	Early entry	0.19	Other than inshore lobsterman	0
			Early entry	0
			Owner/skipper	−0
			Marital status	0
Time/trip length	Average length of fishing trip	−0.35	Ethnicity	0
			Other than inshore lobsterman	−0
			Age	0
			Early entry	0
			Years fishing	−0
Adventure	Fish for cod	0.16	Ethnicity	−0
			Early entry	0
			Father fishes	−0
Offshore	Fish with scallop drag	−0.14		
Time/family	Hours fishing in average week	−0.33		
Crowding	Fish with hook and line, lobster traps	−0.12		

[a] These predictors are all results taken from step-wise multiple regression. amount of variance in the dependent variable will enter first; the variable that second, and so on. In other words, the variable that explains the greatest am equation at each step. And one or more variables may never be entered into th used Pollnac and Poggie's (1979, p. 26) criteria of an *F*-ratio to enter of 2.0 a

he Nova Scotia and New England samples.

		Sample			
s fishermen		Point Judith, Rhode Island		New Bedford, Massachusetts	
		Owner/skipper	0.31	Education	0.44
		Dependents	0.23	Owner/skipper	0.38
re		Father fishes	0.25	Foreign born	0.50
	0.36	Change fish type	−0.31	Still fishing	0.33
	0.16	Relatives fishing	−0.25	Early entry	−0.44
	−0.13				
	0.13				
	0.42	Change fish type	−0.30	Advise young man to fish	0.54
re		Still fishing	0.31	Age	0.44
	−0.26	Relatives fishing	0.31	Early entry	0.32
	0.21	Medium fish trip length	0.26		
	0.18	Advise young man to fish	0.26		
	−0.15				
	−0.56	Early entry	0.29	Still fish	0.43
	0.18	Advise young man to fish	0.26	Father fishes	−0.40
	−0.14				
				Marital status	0.53
				Father fishes	0.33

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ression. As Nie et al. (1975, p. 345) described it, the "variable that explains the greatest
able that explains the greatest amount of variance in conjunction with the first will enter
atest amount of variance unexplained by the variables already in the equation enters the
d into the regression equation if the statistical criteria were not met." In our case, we have
of 2.0 and an increase in explained variance of at least 1.0.

TABLE 8. Comparison (%) of southwest Nova Scotia fishermen with two Maritime samples on overall work satisfaction.[a]

	Sample		
Overall work satisfaction	Southwest Nova Scotia fishermen[b]	General Segmentation sample[c]	Marginal Work World sample[c]
The best job you've ever had	41.4	25.1	13.1
One of the best jobs you've ever had	18.7	25.2	21.1
Above average job	9.8	15.0	17.3
Average job	26.8	30.8	38.9
Below average job	1.7	3.0	6.1
One of the worst jobs you've ever had	1.0	0.5	2.1
The worst job you've ever had	0.7	0.4	1.4
	(418)[d]	(930)[d]	(427)[d]

[a] The Marginal Work World study is a 1977–78 survey of 587 private-sector *low-wage* workers in the three Maritime provinces (R. Apostle, D. Clairmont, and M. MacDonald, Institute of Public Affairs, Dalhousie University, Halifax, N.S., unpubl. data). The General Segmentation study is a 1979 survey of 1513 workers employed throughout the private sector in these provinces (R. Apostle, D. Clairmont, and L. Osberg, Institute of Public Affairs, Dalhousie University, Halifax, N.S., unpubl. data).

[b] The question reads "17. Overall, how satisfied are you with fishing?"

[c] The question reads "Overall, how satisfied are you in working there?"

[d] The responses for the southwest Nova Scotia fishermen and the Marginal Work World sample include only those who have held more than one job, and the answers for the General Segmentation sample include only those who have had more than one employer. If one includes those who have only had one job or employer, the percentages are 51.0, 17.0, 8.4, 21.1, 1.2, 0.7, and 0.5 (582); 19.8, 24.4, 15.9, 34.6, 3.6, 1.0, and 0.6 (1437); and 15.2, 18.6, 18.5, 36.7, 5.5, 2.6, and 2.9 (549), respectively.

The R^2 value, or the amount of variance in the dependent variable jointly accounted for by the independent variables, is a rather small 20.3%. This low figure is probably attributable, at least in part, to the absence of hard information on income (which we found was too sensitive an issue to risk asking questions about in this study), as well as the lack of variation on occupational status and education levels within this particular occupational group.

Community Attachments

Job satisfaction alone is not able to explain attachment to the fishery. The decision to remain or leave is related to other considerations, such as the opportunity for alternative employment, and kin and community ties. In order to examine these, a number of questions concerning kin and community were included in the questionnaire. These were designed to see if generalizations derived from community studies (A. Davis, Anthropology Department, University of Manitoba, Winnipeg, Man., unpubl. data) which show a strong commitment to kin, community, and occupation, combined with a high degree of job satisfaction, are general to the whole of southwest Nova Scotia. If they are, this will establish southwest Nova Scotia as a population distinct from the three populations found in New England.

Our sample shows a high degree of continuity in community composition. Fifty-six percent have lived in their community since birth. Of those who moved into the community, 46% came from within 10 mi (16 km) or less, and 30% came from within 11–50 mi (18–80 km). These figures imply a high degree of social and cultural homogeneity. This is directly substantiated by the sharp geographic boundaries between Protestant and Catholic communities in this area which largely corresponds to a division between English- and French-speaking areas. For example, Barrington Municipality in Shelburne County, and Argyle Municipality in Yarmouth County, are adjacent to one another. Both are characterized by having numerous fishing communities dominating their economies. However, the former is almost completely English-speaking and Protestant, while the latter is almost completely French-speaking and Catholic.

There is a high degree of satisfaction with the community in which the fishermen live. Sixty-nine percent feel they "really belong here," 28% feel they "belong here," and only 3% feel they do not belong "very much," or "not at all." Sixty-five percent were very satisfied with their community, 28% "moderately satisfied," and only 7% either neutral or showing some degree of dissatisfaction.

One measure of community integration is degree and quality of interaction between members. This is particularly important where fishing is the dominant occupation, as effective participation in the fishery depends on a network of kin and neighbors for information, aid, and in some cases actual access to resources. In communities such as these, which are relatively small and where most people spend all their lives in the same one, a high percentage of members will be kinsmen and interaction with them and with neighbors will tend to be frequent and intense. In our study, 52% of respondents know all of their neighbors well, 26% know most well, 11% know some well, and 9% a few well. Only 2% know none well.

The skills which fishermen have and the technologies they employ are potentially mobile. Eighty-eight percent of the respondents agreed that they could continue to fish if they had to move from their present harbour. However, when asked what they would do if offered better jobs at varying distances from their present place of residence, there was a very strong and

TABLE 9. Significant predictors of overall work satisfaction. ***Significant at the 0.001 level.

Significant predictors	Overall work satisfaction
Independence	0.23***
Religion[a]	−0.22***
Earnings	0.21***
Part-time/full-time license	0.16***
Respondents	400
$R^2 \times 100$	20.3[b]

[a] We recoded our religious denomination question in terms of religious orthodoxy to create this variable. Conservative Protestants (Baptist, Pentecostal, Lutheran, and Salvation Army) are scored 1, Catholics (Roman Catholics, Ukrainian Catholics) are scored 2, liberal Protestants (United Church, Anglican, and Presbyterian) are scored 3, and those with no religion (no religious beliefs, agnostic, atheist) are scored 4. The percentage distribution for the specific denominations as listed are 37.6 (Baptist), 3.9, 1.5, 0.3, 21.8 (Roman Catholic), 0.2, 12.8 (United Church), 12.4, 0.7 and 2.7 (no religious beliefs), 1.3, and 1.0. The remaining 3.7% of our 595 respondents with specified denominations belonged to other unclassifiable groups, and are excluded from this analysis.

[b] This figure represents the amount of variance in the dependent variable jointly accounted for by the four independent variables.

pervasive commitment to remaining in their present place of residence. This commitment increased in relation to the distance from home community of postulated better job elsewhere. Seventy-one percent would stay if offered a better job in Nova Scotia, 75% in another Maritime province, and 82% if the job was elsewhere in Canada. Although skills and technologies are portable, community and kin-based social networks are not. This is to suggest that the extreme reluctance to move documented above may be based on a rational calculation of gain as well as on more subjective psychological and emotional factors. In other words, in addition to emotional ties, there may be a greater loss in leaving a home community than the gains defined by the term "better job."

The very strong commitment to community documented above could be realized by occupations other than fishing, or by combining fishing with one or more additional occupations ("occupational pluralism"). For example, in some areas of Maine, forestry is a supplement to fishing. However, due to ecological conditions, such options are on the whole not available to the fishermen of southwest Nova Scotia. Thus, 75% of our sample derived 100% of their 1981 income from fishing. Only 10% derived less than 40% of their 1981 income from fishing. In this area, fishing tends to be an occupation characterized by a higher degree of exclusive dependence than in other areas. Fishermen in southwest Nova Scotia have other characteristics which also demonstrate a higher degree of social integration than the other two Maritime samples referred to above. By comparison, there are fewer single people and more married ones. In addition, our sample has more children and a higher percentage of home ownership. Since land for building and help in materials and labour in rural Nova Scotia are frequently obtained from kin and/or neighbors, the differences are indicative of denser social networks among fishermen. A consequence of dense networks is a high degree of social and psychological support which is reflected back onto the community in such things as feelings of belongingness.

The importance of family, kin, and community documented thus far is related to a very high degree of occupational continuity. This is an economy where there is a strong tendency towards generational succession in occupation, with fathers passing on their skills and knowledge to their sons. We found that 48% of our sample have fathers now fishing, and even this figure underestimates generational continuity because fishermen tend to leave active fishing at a relatively early age. In addition, 57% of the fishermen have one or more brothers who fish, 57% have one or more uncles who fish, and 66% have one or more first cousins who fish. While these relatives may not be sources of financial support (banks and government agencies have largely replaced merchants and kin as sources of capital), intangible capital in the form of exchanges of knowledge and experience, as well as possibilities of mutual aid, are consequences which flow from generational succession.

Conclusions

Poggie and Pollnac's studies of the New England situation reveal three types of attachment to the fisheries based on port location and characteristics:

(1) Ports such as Point Judith, Rhode Island, where high job satisfaction characterizes fishermen, but where ties to kin and community are weak.

(2) The ethnic ports of southern New England, where commitment to the fishery is weak, but where participation in the industry provides the economic support which maintains strong kin and status positions within the community (e.g. New Bedford, Massachusetts, and Gloucester, Massachusetts).

(3) Maine, where connections to the fishery are also weak, but where people remain in the fishery because it makes the maintenance of kin and community ties possible. These differences are striking and have obvious impacts for intergenerational continuity in the fisheries, especially in the major ports of southern New England.

When comparing our profile of southwest Nova Scotia with the above we concluded the following:

(1) Southwest Nova Scoia fishermen, like those in Maine and New Bedford, are strongly attached to their communities.

(2) Like those of Rhode Island, they are strongly attached to fishing as an occupation.

(3) In contrast with the Rhode Island fishermen, thoses of southwest Nova Scotia combine love of fishing as an occupation with strong attachment to community.

(4) In contrast with the fishermen of Maine and New Bedford, they are equally attached to both kin and community and to fishing as an occupation.

Southwestern Nova Scotia fishermen share certain characteristics with the three New England populations. They combine them in such a way as to justify their being treated as a distinct fourth population.

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Gas Supersaturation as a Cause of Early Spring Mortality of Stocked Trout

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Rainbow trout (*Salmo gairdneri*) fingerlings, stocked through the ice of shallow prairie lakes, experienced high mortality even though algal photosynthesis had returned whole-lake oxygen concentrations to normal levels prior to ice melting. Fish caged beneath the ice showed symptoms of asphyxiation or gas bubble disease, depending on depth. Asphyxiation occurred at oxygen concentrations below 4 mg/L. We identify total dissolved gas tension as the primary cause of bubble disease and resulting mortality, and demonstrate the relative contribution of oxygen and nitrogen to total gas tension. Significant mortalities were associated with oxygen relative partial pressures (gas partial pressure relative to total hydrostatic pressure) exceeding 0.2, but only when accompanied by nitrogen relative partial pressures above 1.1. Total relative gas tension under these circumstances exceeded 1.3. An increase in nitrogen partial pressures over the winter was attributed to the physical freeze-out of nitrogen from the ice in shallow lakes where reduction of lake volume due to ice formation is substantial.

Des tacons de truite arc-en-ciel (*Salmo gairdneri*), libérés à travers la glace de lacs peu profonds des prairies, ont subi une mortalité élevée même si la photosynthèse algale avait ramené les teneurs en oxygène à des niveaux normaux avant le dégel. Les poissons gardés en cages sous la glace ont montré des signes d'asphyxie ou d'aéroembolisme à cause de la profondeur. L'asphyxie est survenue à des teneurs en oxygène inférieures à 4 mg/L. La tension totale en gaz dissous est identifiée comme étant la cause principale de l'aéroembolisme et de la mortalité qui s'ensuit ; en outre, la contribution relative de l'oxygène et de l'azote à la tension gazeuse totale est expliquée. Un nombre élevé de mortalités a été attribué à des pressions partielles relatives de l'oxygène (pression gazeuse partielle par rapport à la pression hydrostatique totale) supérieures à 0,2, mais seulement avec des pressions partielles relatives de l'azote supérieures à 1,1. Dans ces circonstances, la tension gazeuse totale relative dépassait 1,3. Une augmentation des pressions partielles de l'azote au cours de l'hiver a été imputée à l'extraction physique de l'azote contenu dans la glace des lacs peu profonds, où la baisse de volume est importante à cause de la formation de glace.

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In central North America, winter fish kills are a common feature of shallow lakes north of about 45°N. Fish mortalities generally occur during February and early March as a result of progressive oxygen depletion beneath the ice during the winter months. Oxygen depletion has been studied in considerable detail during the past 35 yr (Greenbank 1945; Scidmore 1957; Welch et al. 1976), and its mechanism as well as predictive models have been recently developed (Barica and Mathias 1979; Mathias and Barica 1980).

The winterkill phenomenon, because it rids lakes of endemic fish and results in a high standing crop of benthic invertebrates, has been the basis for extensive trout culture in shallow lakes of the Canadian prairies (Lawler et al. 1974). In this type of aquaculture, fingerling trout are planted in the early spring and harvested in the fall of the same year. Ice cover normally disappears in mid-April, and it has been assumed that the recovery of normal dissolved oxygen levels due to photosynthesis by late March (Barica and Mathias 1979) would render them suitable for the stocking of fingerlings beneath the ice. Three advantages would be gained: first, fingerlings would have time to recover from stocking stress and acclimate to lake conditions well before onset of the increasing spring water temperatures which yield maximum growth (Bernard and Holmstrom 1978); second, during their period of acclimation, fingerlings would be protected from predation by migratory terns which move through the area during April (Ayles et al. 1976); and third, the growing season would be extended by 2–4 wk.

Recently, however, we have observed high trout mortality in ice-covered prairie lakes well after whole-lake oxygen concentrations have returned to normal levels. This phenomenon presents a serious obstacle to trout culturists who wish to take advantage of early stocking.

In an earlier, preliminary presentation (Lark et al. 1979) we attributed the cause of fish mortality solely to oxygen supersaturation under the ice. In this paper, we reanalyze the results and present an alternative hypothesis, suggesting that total gas tension is the primary cause of mortality, and identifying dissolved nitrogen as well as dissolved oxygen as the principal gas components, contributing to the gas bubble disease phenomenon.

Methods

Lakes

The lakes studied are in the vicinity of Erickson, southwestern Manitoba, at approximately 50°30′N, 100°10′W. Some characteristics of the lakes (Barica 1975a) are as follows:

Lake (no.)	Area (ha)	Mean depth (m)	Specific conductance (μS/cm)
885	2.4	1.9	1395
154	10.1	2.3	1220
318	21.9	1.4	787
721	6.5	1.6	3443

Lakes 154, 318, and 721 are typical of those used for trout aquaculture and have successful trout production records. In all of the lakes, winter anoxia is a common phenomenon. Lake 885, a highly eutrophic lake, experiences periodic summer anoxia as well, due to the annual collapse of algal blooms (Barica 1975b). Additional limnological data for these lakes and description of the area can be found in Sunde and Barica (1975).

Experimental Study Design

At the time of testing (April 1977) all lakes had 5–10 m of open water around the shore, although the ice was still thick enough to walk upon. The 24-h survival of rainbow trout (*Salmo gairdneri*) in cages and depth profiles of water chemistry were measured at two locations in each lake: at the center (deep station) and close to open water near the shore (shallow station). Measurements were repeated at 4- to 8-d intervals on each lake until water conditions were adequate for trout survival over 24 h.

Experimental fish cages were 0.5 × 0.5 × 0.1 m deep, made from mesh nylon netting with a 0.64-cm mesh, and confined fish to 0.1-m water layers. In a typical deepwater test, five cages were suspended at different depths on a common rope. The depths were chosen after determining the vertical oxygen distribution at the test site. After being lowered through the ice the cages were moved about 6 m horizontally to avoid the disturbed water column beneath the ice hole. Five cages were used at deepwater sites and three cages at each shallow site. Tests were always begun between 14:00 and 16:00.

Rainbow trout fingerlings (10 g wet weight) were obtained from the Freshwater Institute Rockwood Trout Hatchery near Gunton, Manitoba. They were hauled for 4 h in a 1.5-m^3 transport tank with continuous oxygen supply and placed in holding cages at about 4°C until required (1–2 d). Fifty fingerlings were placed in each experimental cage and examined after 24 h to ascertain percent survival and cause of death.

Symptoms of asphyxia, characteristic of fish held in low-oxygen water, were notable by pale body colouration, absence of parr-marks, widely flared gills and jaws, and head raised dorsally. Symptoms of gas bubble disease included bubbles beneath skin, slightly protruding eyeballs, very dark colouration with parr-marks frequently distinct, gills and jaws closed, and trunk bent laterally.

Water Chemistry Monitoring

Vertical profiles of temperature and dissolved oxygen were determined before and after deployment of cages in April 1977. At the beginning of each 24-h test, the following additional measurements were made at 0.5-m depth intervals: ammonia nitrogen, hydrogen sulphide, chlorophyll *a*, conductivity, and redox potential. Single samples were also taken for pH, carbonate, and bicarbonate. All water samples were immediately analysed at a field laboratory following the methods of Stainton et al. (1974). Redox potential was measured in situ with an Orion electrode, model 96-78-00. Lake volumes were calculated from morphometric charts given in Sunde and Barica (1975).

Dissolved nitrogen was measured beneath the ice of three of the lakes (885, 154, and 318) in spring 1982. Water samples were collected from discrete depths directly into 10-mL glass syringes which were then sealed under water and stored on ice. Dissolved oxygen at the same depth was measured by the Winkler technique, in situ temperatures were measured with a thermistor, and ice thickness was recorded. The syringe contents were brought to 25°C and transferred via a valve manifold (helium-purged) to a 50-mL glass syringe (helium-purged) to which 40 mL of helium was then added. After agitation for 20 s, the gas phase was injected into a gas chromatograph sample loop (2 mL) and then into a 2-m "molecular seive 5A" column for separation and detection of oxygen and nitrogen.

Gas Saturation

Calculations of gas saturation were based on work by Ricker (1934), who devised a critical measure of oxygen saturation at which bubbles would tend to grow in water. Ricker's critical oxygen concentration took into account hydrostatic pressure as well as the partial pressure of nitrogen. His basic formulation, corrected by Hutchinson (1957) for water vapour pressure, was

$$(1) \quad x' = q_o\left(\frac{P_z - P_w}{P_0} - \frac{n}{q_n}\right)$$

where x' = a critical concentration of oxygen (mg/L) at which bubbles would tend to grow, P_z = total pressure (mmHg) at depth z, including both atmospheric plus hydrostatic pressure (note: 1 mmHg is equivalent to 133.3224 Pa), P_w = partial pressure of water vapour at ambient water temperature, P_0 = 750 mmHg, n = concentration of dissolved nitrogen (mg/L), and q_o and q_n = solubility of oxygen and nitrogen respectively, in water equilibrated with an atmosphere of the pure gas at 760 mmHg and ambient temperature.

We have used a more general expression of equation 1 (see Discussion) in which the sum of the partial pressures of nitrogen and oxygen (relative to the total hydrostatic pressure) is compared with unity. Both sides of the equation were divided by q_0, rearranged, and then divided by $(P_z - P_w)/P_0$ to give

$$(2) \quad 1.0 = \frac{P_0}{P_z - P_w}\left(\frac{x}{q_o} + \frac{n}{q_n}\right)$$

where x = concentration of dissolved oxygen (mg/L) and $xP_0/(P_z - P_w)q_o$ = the partial pressure of oxygen in atmospheres, i.e. xP_0/q_o, expressed as a fraction of the total atmospheric and hydrostatic pressure $(P_z - P_w)$ at depth z.

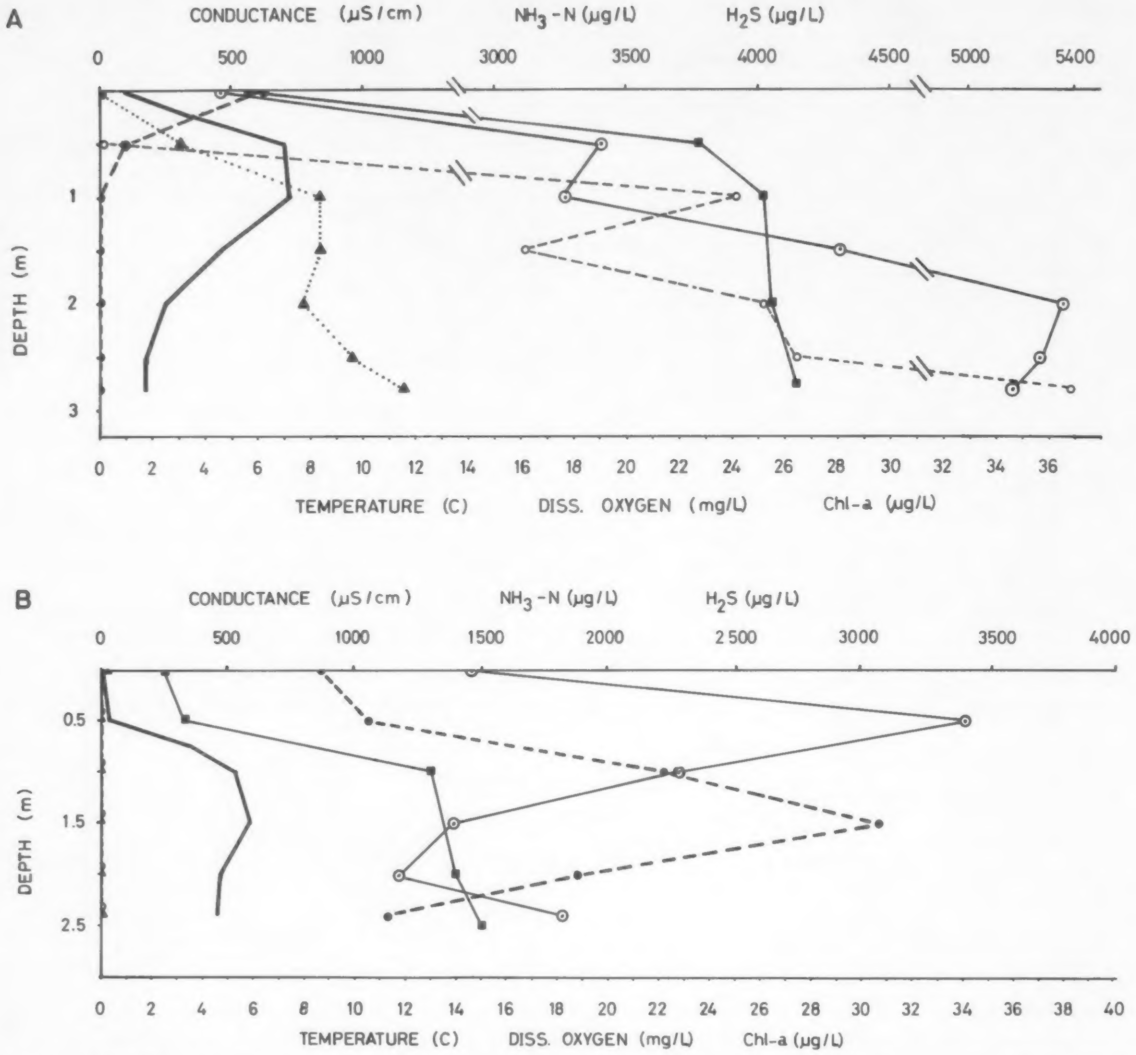

FIG. 1. Vertical distribution of hydrogen sulphide (○), ammonia (▲), chlorophyll *a* ⊙, specific conductance (■), temperature (solid line), and dissolved oxygen (●) in study lakes immediately before icemelt. (A) Lake 721, April 15; (B) lake 318, April 14; (C) lake 154, April 13; (D), lake 885, April 14, 1977.

This latter quantity may be termed the relative partial pressure of oxygen. When the right-hand side of the equation 2 (i.e. the sum of the relative partial pressures of oxygen and nitrogen) is greater than 1.0, there is a tendency for bubbles to grow, and when it is less than 1.0, bubbles should dissolve.

Freeze-Out Model

According to Barica (1977), the physical process of solute freeze-out in a shallow land-locked lake can be described by the following equation:

$$(3) \quad \frac{C_x}{C_0} = \frac{V_0}{V_x}$$

where C_x = concentration of solute at time of maximum ice thickness, C_0 = concentration of solute prior to ice formation, V_x = lake volume (liquid phase) at time of maximum ice thickness, and V_0 = lake volume prior to ice formation.

This suggests that any decrease in volume (liquid phase) of a lake due to ice formation will be accompanied by a corresponding, proportional increase in the concentration of solute. According to this model, elevated concentrations of dissolved nitrogen are predicted as a result of freeze-up. The model assumes an insignificant mass of solute remaining in the ice, and complete solubility of the solute in the new volume V_x.

Results

Water Chemistry

During the last few days of ice cover, all four lakes showed considerable vertical structure, both chemical and physical.

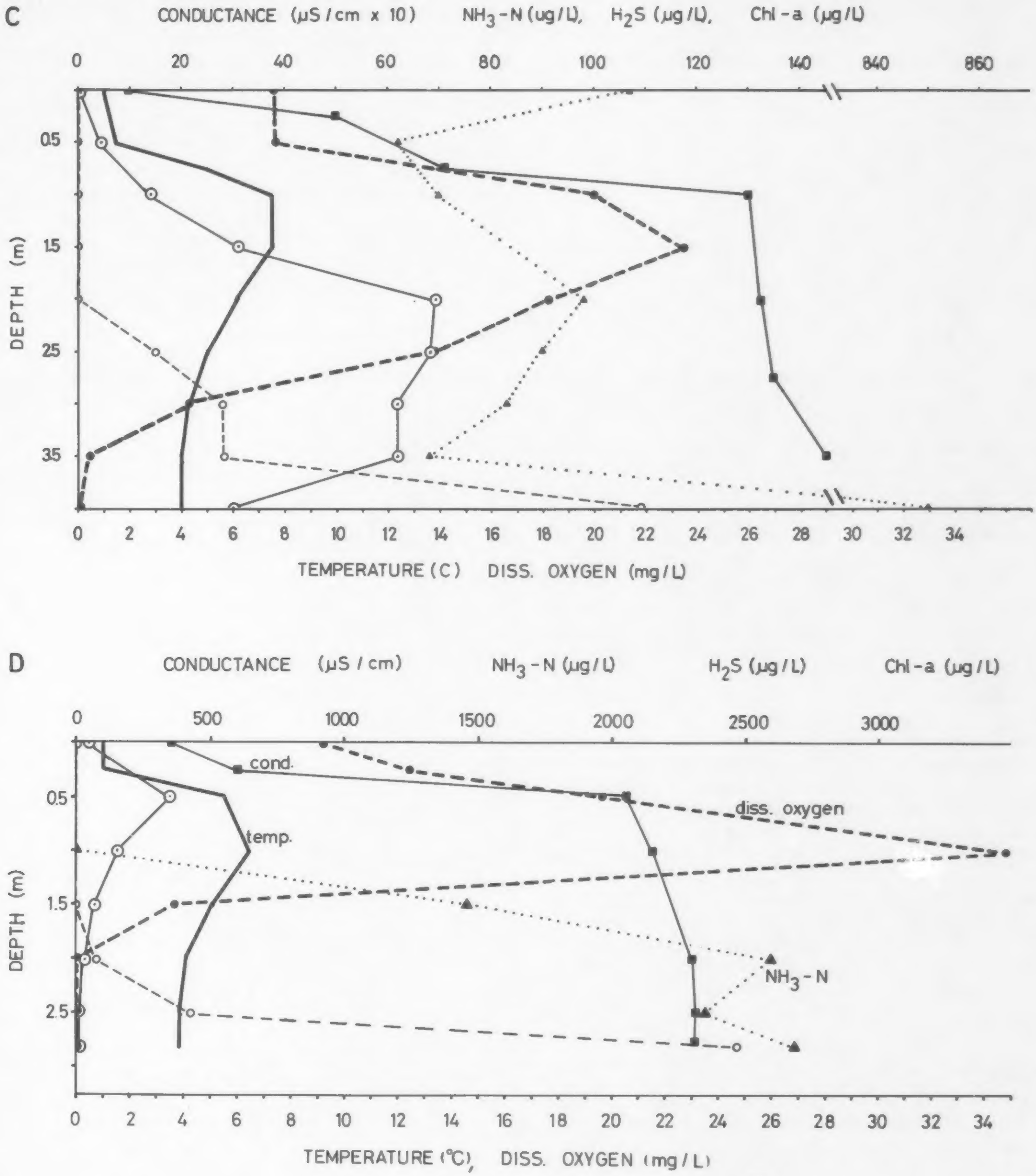

FIG. 1. (*Concluded*)

Water temperatures were held below 1°C by meltwater near the ice–water interface, and were at or below 4°C at the lake bottom (Fig. 1). At intermediate depths, particularly 0.5–1.5 m, significant warming had taken place in all lakes, presumably a result of absorption of solar radiation by dense algal blooms in the upper water column (algal biomasses of 6000 – 30 000 µg/L were found at depths less than 1.0 m; Table 1). The stability of these anomalous temperature distributions was maintained by water density gradients found between the lower ice boundary and 1.0 m (all lakes), and near the sediment (lake 721). Specific conductance in the four lakes varied from 100–550 µS/cm at the lower ice boundary to 1300–2150 µS/cm at a depth of 1.0 m (Fig. 1), indicating the meltwater layer. The elevated temperature found at intermediate depths is noteworthy, because it would be expected to decrease the solubility of gases at that depth, while increasing the rate of biological activity. Both phenomena could lead to higher gas tensions.

The concentration of chlorophyll *a* was high beneath the ice

TABLE 1. Phytoplankton biomass (g/m^3) in three of the study lakes. Dashes indicate that no sample was taken. Lake 154 was not sampled.

Depth (m)	Lake 721 (Apr. 15, 1977)	Lake 318 (Apr. 14, 1977)	Lake 885 (Apr. 14, 1977)
0	0.1	8.3	10.7
0.25	1.5	—	—
0.5	30.7	—	—
1.0	—	6.2	23.8
2.0	—	4.3	4.6

of all four lakes, the maximum ranging from 34 to 350 μg/L. Primary production was also high in three of the lakes, resulting in dissolved oxygen concentrations from 23 to 34 mg/L (Fig. 1B–1D). These values were well above the oxygen saturation of water in equilibrium with air (about 13 mg/L). High rates of oxygen production were restricted to narrow depth zones 0.5–1.5 m in width which corresponded to the depths of maximum water temperature (Fig. 1). Oxygen supersaturation was not observed in lake 721, despite the high chlorophyll *a* concentration and algal biomass observed at 0.5 m, because of its high concentration of hydrogen sulphide and resulting high chemical oxygen demand.

Under-ice photosynthesis, superimposed upon the typically anoxic water column of these lakes during the winter, separated them into three categories with regard to oxygen distribution: *hypoxic* - lake 721 where most of the water column was oxygen-poor; *hyperoxic* - lake 318 where the water column was largely supersaturated; *layered* - lakes 154 and 885 where oxygen-supersaturated water overlaid an oxygen-poor water layer.

The oxidizing effect of dissolved oxygen was reflected in the vertical distribution of dissolved hydrogen sulphide and ammonia (Fig. 1). Except for the 2.0–3.0 m layer in lake 154, hydrogen sulphide was never present when the dissolved oxygen concentration was higher than 1.0 mg/L, and there was a general inverse relationship between NH_3–N and dissolved oxygen.

Physical and chemical data for stations near the edge of the ice pan are more or less similar to the data presented for central lake stations in Fig. 1, and the correspondence between them will be treated by J. A. Mathias (in prep.). Except for lake 721, vertical stratification disappeared soon after the ice melted (Table 2), and water quality for trout improved.

Fish Mortality

Mortality of rainbow trout held in cages was substantial in all lakes, and restricted largely to the period of ice cover (Table 3). Ammonia and hydrogen sulphide toxicity could be largely discounted as primary causes of mortality. Toxic levels of these substances were associated invariably with oxygen concentrations low enough to cause asphyxiation within a matter of minutes. For example, hydrogen sulphide rose to toxic levels only when the redox potential fell below +100 mV (Fig. 2). Except for one datum (redox potential +63 mV, oxygen 1.0 mg/L), oxygen was not detectable at these redox potentials. Similarly, the highest ammonium concentrations observed (lake 885) ranged from 1.4 to 2.7 mg/L in the absence of measurable dissolved oxygen, and from 0.5 to 0.8 mg/L in oxygenated water. These corresponded to toxic, undissociated ammonia concentrations of 0.1–0.2 and 0.05–0.07 mg/L, respectively, at the ambient temperature (4.0–7.5°C) and pH (8.8) observed. The lowest undissociated ammonia concentration known to cause mortality in rainbow trout fingerlings is 0.2 mg/L (EIFAC 1970). Therefore, concentrations that could have caused mortality in lake 885 were also associated with anoxic conditions.

On the other hand, fish mortality was closely related to the dissolved oxygen concentration (Fig. 3). Two causes of death were identified. At oxygen concentrations below 5 mg/L, all dead fingerlings showed symptoms of asphyxia. Above 10 mg/L, all under-ice mortality was associated with symptoms of gas bubble disease. The few fish that died between these limits showed no identifiable symptoms. After the ice had melted and the lakes were subject to wind mixing, most mortality was restricted to oxygen-poor water layers near the sediments. Lake 721, for example, remained poorly mixed for about 2 wk subsequent to icemelt, and deepwater oxygen concentrations remained inadequate for trout survival during this period (Table 1).

Nitrogen Freeze-Out Hypothesis

Pronounced symptoms of gas bubble disease in dead fish were associated with dissolved oxygen concentrations in excess of 18 mg/L. However, less-pronounced symptoms (dark colouration, contraction of skeletal musculature) were observed at

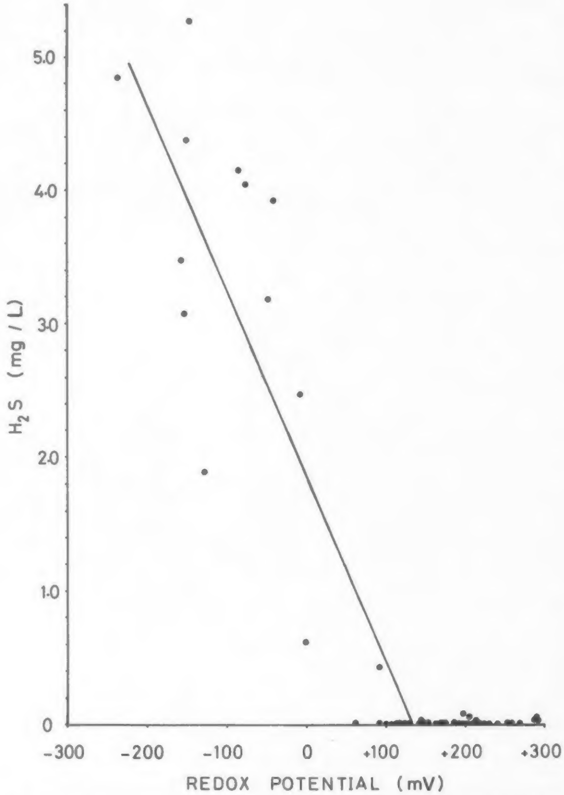

FIG. 2. Redox potential and concentration of hydrogen sulphide in water samples from study lakes. Data were combined from all depths, lakes, and sample periods (April 13–22, 1977). Line was fitted by regression.

TABLE 2. Depth distribution of water quality parameters in study lakes immediately after icemelt. Dates of icemelt: lake 885, April 17, 1977; lake 154, April 20, 1977; lake 318, April 18, 1977; lake 721, April 17, 1977.

Depth (m)	Temperature (°C)	Dissolved oxygen (mg/L)	Redox potential (mV)	H_2S (μg/L)	NH_3 (μg/L)	Chlorophyll *a* (μg/L)
Lake 885 (Apr. 19, 1977)						
0	8.4	15.5	125.5	0	533	92.2
0.5	8.4	14.9	120.4	0	771	116.9
1.0	8.1	14.4	119.2	0	558	106.4
1.5	8.0	13.7	—	0	778	91.8
2.0	7.0	13.3	122.7	0	598	64.9
2.5	7.0	12.3	126.0	0	867	57.3
2.9[a]	5.9	3.3	144.7	0	1505	28.6
Lake 154 (Apr. 21, 1977)						
0	6.0	11.0	214.7	—	0	23.1
0.5	6.0	—	—	—	—	—
1.0	6.0	11.1	216.4	—	0	28.5
1.5	6.0	11.4	—	—	—	—
2.0	6.0	11.4	217.1	—	0	29.4
2.5	6.0	11.5	—	—	—	—
3.0	6.0	11.5	218.0	—	0	29.5
3.5	6.0	11.5	220.9	—	0	25.6
4.0[a]	6.0	10.8	224.3	—	0	25.7
Lake 318 (Apr. 20, 1977)						
0	5.0	12.4	244.6	0	0	26.5
0.5	5.0	12.4	230.0	0	0	26.4
1.0	5.0	12.5	228.0	0	0	25.7
1.5	5.0	12.4	226.6	0	0	25.8
2.0	5.0	12.4	229.9	0	0	25.8
2.5[a]	5.0	11.7	230.3	0	0	53.2
Lake 721 (Apr. 19, 1977)						
0	9.8	6.8	225.6	0	267	14.8
0.5	9.8	7.1	221.9	0	260	9.4
1.0	9.8	5.7	220.7	0	275	16.6
1.5	7.6	0.3	205.6	41	595	13.6
2.0	4.2	0.3	−127.8	1889	612	67.5
2.5	2.6	0	−235.6	4843	896	113.4
2.8[a]	2.5	0	−290.5	5736	970	72.1
Lake 721 (Apr. 27, 1977)						
0	13.0	10.8	209.9	—	0	15.0
0.5	13.0	—	—	—	—	—
1.0	12.9	10.8	—	—	—	—
1.5	12.9	10.8	210.4	—	0	17.6
2.0	10.6	4.5	231.6	—	145	71.3
2.5	6.0	0.2	—	—	—	—
2.8[a]	4.0	0	83.4	—	942	363.6
Lake 721 (May 4, 1977)						
0	14.6	8.4	176.2	0	0	14.5
0.5	14.3	—	—	—	—	—
1.0	14.3	8.5	174.6	0	0	16.7
1.5	14.2	8.5	175.2	0	0	18.6
2.0	13.5	7.9	177.2	0	1	22.3
2.5	11.8	7.7	172.4	0	6	24.1
2.8[a]	8.5	0	169.1	194	39	201.4

[a] Refers to lake bottom.

TABLE 3. Percent mortality of rainbow trout caged for 24 h at selected water depths. Ice is present on the earliest date shown for each lake.

Depth (m)	Lake 885		Lake 154		Lake 318		Lake 721			
	Apr. 14	Apr. 19	Apr. 13	Apr. 21	Apr. 14	Apr. 21	Apr. 15	Apr. 19	Apr. 27	May 4
0		16				0		0	0	0
0.5	61	0	0	0	6		0	0		
1.0	100				33	4	100	0		
1.5	22	2	96	0	98	0	100	100	0	0
2.0	100				92	0	100		0	0
2.5		0	4	0	4	2			100	0
2.8	98	100					100	100	100	100
2.9										
3.0			100	0						
4.0			100	2						

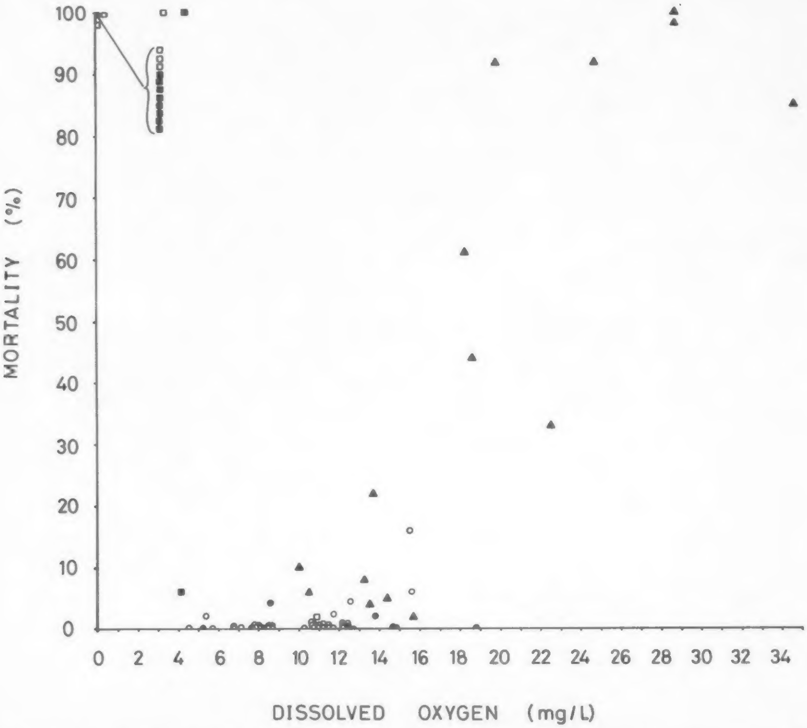

FIG. 3. Percent mortality of caged trout in relation to average dissolved oxygen concentration over 24 h. Data combined for all study lakes. Solid symbols, cages under ice; open symbols, cages in open water; triangles, fish show symptoms of gas bubble disease; squares, fish show symptoms of asphyxiation; circles, fish show no symptoms.

oxygen concentrations of 10–16 mg/L. These observations suggested that oxygen was not the primary gas causing bubble disease. since other dissolved gases (NH_3, H_2S) were at low concentrations, and CO_2 was also low at the high pH recorded, we assumed that nitrogen must have been in excess. Although nitrogen was not measured during the 1977 experiments, we hypothesized, following the freeze-out model of Barica (1977, equation 3), that during the ice-covered portion of the experiment the water was supersaturated with dissolved nitrogen as a result of exclusion from the ice layer.

To test this hypothesis, we estimated dissolved nitrogen concentrations based on the freeze-out model and compared these estimates with actual measurements made on three of the lakes (154, 885, and 318) just prior to icemelt in 1982.

Our estimates of the dissolved nitrogen concentration at freeze-up in the fall of 1981 (Table 4) were taken from atmospheric nitrogen solubility tables of Rucker (1972, after Weiss 1970) and converted from millilitres per litre to milligrams per litre using a conversion factor of ×1.267 (Ricker 1934). We assumed that the surface water temperature during

TABLE 4. Prediction of dissolved nitrogen concentrations beneath the ice in spring of 1982, based on the nitrogen freeze-out model.

	Lake		
	154	885	318
Water temperature at freeze-up, 1981 (°C)	1.4	2.8	2.8
N_2 solubility at 760 mmHg (mL/L)	18.25	17.61	17.61
Estimated dissolved N_2 concentration, fall 1981, at lake altitude (mg/L)	21.35	20.61	20.61
Maximum ice thickness, 1982 (m)	0.75	0.62	0.75
Lake volume at freeze-up (V_0)/ lake volume at maximum ice thickness (V_x)[a]	1.484	2.312	1.768
Predicted dissolved N_2 concentrations under spring ice, 1982 (mg/L)	31.68	47.65	36.44

[a] See equation 3.

gaseous equilibration with the atmosphere immediately prior to freeze-up was equal to the lowest temperature observed in each lake. The estimates were corrected for atmospheric pressure at the altitude of the lakes (640 m) using equation 4 (Hutchinson 1957) and corrected for the partial pressure of water using equation 5:

$$(4) \quad \log P_h = \log P_0 - \frac{273h}{18\,421\,(T_0 + 273 + 0.0025h)}$$

$$(5) \quad K_h = (P_h - P_w)/(760 - P_w)$$

where K_h = correction factor applied to nitrogen solubility tables, P_h = atmospheric pressure (mm) at any altitude, h, P_0 = 760 mmHg atmospheric pressure at sea level, h = altitude (m), T_0 = surface water temperature of lake during gaseous equilibration with the atmosphere, and P_w = partial pressure of water vapour at temperature T_0.

Dissolved nitrogen concentrations, predicted by the freeze-out hypothesis (Table 4), were then compared with actual measurements under the ice of three lakes in April 1982 (Fig. 4). Despite considerable variability in the data, observed values correlated strongly with predicted values (correlation coefficient = 0.90, $p < 0.01$), indicating that the freeze-out model could be used to estimate dissolved nitrogen concentrations in 1977 when measurements were not taken. The freeze-out model, however, can only be applied to deeper water layers which have not been diluted by melting ice-water. (In the meltwater zone between the lower ice boundary and 0.5 m, average dissolved nitrogen concentrations were at atmospheric equilibrium.) In 1977, these undiluted water layers, identified by high and uniform conductivities (Fig. 1), were located below 0.5 m in lakes 885 and 721 and below 1.0 m in lakes 154 and 318.

To correlate the tendency for bubble formation (from equation 2) with our 1977 fish mortality data, it was necessary to estimate the dissolved nitrogen concentration for the spring of 1977 as in Table 5, using the nitrogen freeze-out model. The partial pressure of nitrogen, estimated in this way, and the partial pressure of oxygen, measured in spring 1977, are plotted in Fig. 5 as a percentage of the total hydrostatic pressure at each depth. The sum of the partial pressures of nitrogen and oxygen is also shown as a percentage of total hydrostatic pressure. Note that the concentration of dissolved nitrogen in the meltwater zone was in gaseous equilibrium with the atmosphere. The meltwater zone is indicated in Fig. 5 as the 25–50 cm cold water layer just beneath the ice.

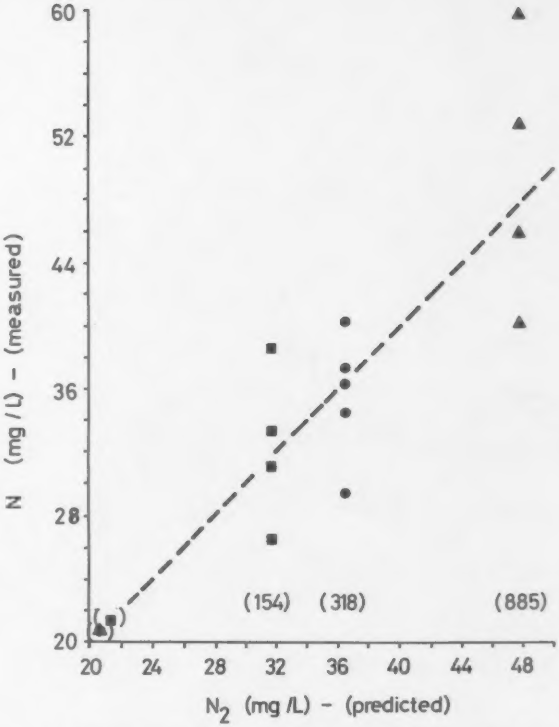

FIG. 4. Dissolved nitrogen concentration measured beneath the ice of lakes 154 (■), 318 (●), and 885 (▲) in 1982 compared to concentrations predicted by the nitrogen freeze-out model. Symbols in parentheses indicate dissolved nitrogen concentration at freeze-up assuming 100% saturation.

Whenever the sum of the gas partial pressures exceeds total hydrostatic pressure, theoretically there is a tendency for bubble growth. The partial pressure of nitrogen alone exceeded total hydrostatic pressure at depths of 1.0 m and greater in lakes 318 and 154 and at depths of 0.5 m and greater in lake 885. The tendency for bubble growth was further augmented by high oxygen partial pressures between 0.5 and 1.5 m in all three lakes (Fig. 5A–5C).

Gas Bubble Disease

In fish caged beneath the ice, gas bubble disease was a function of total gas tension rather than a result of oxygen or nitrogen supersaturation alone. This may be seen by plotting trout mortality (under-ice mortality where the cause of death was, or could have been, due to gas bubble disease, i.e. all solid points beyond 10 mg/L oxygen in Fig. 3) as a function of both the relative partial pressures of oxygen and of nitrogen (from Fig. 5). Significant mortality was associated with oxygen relative partial pressures exceeding 0.2 (Fig. 6), but only when accompanied by nitrogen relative partial pressures above 1.1. Total relative gas tension under these circumstances exceeded 1.3 as shown by the diagonal line in Fig. 6. When percent fish mortality in cages ($n = 21$) was regressed against ambient gas tension, the degree of correlation and the F factor (ratio of mean

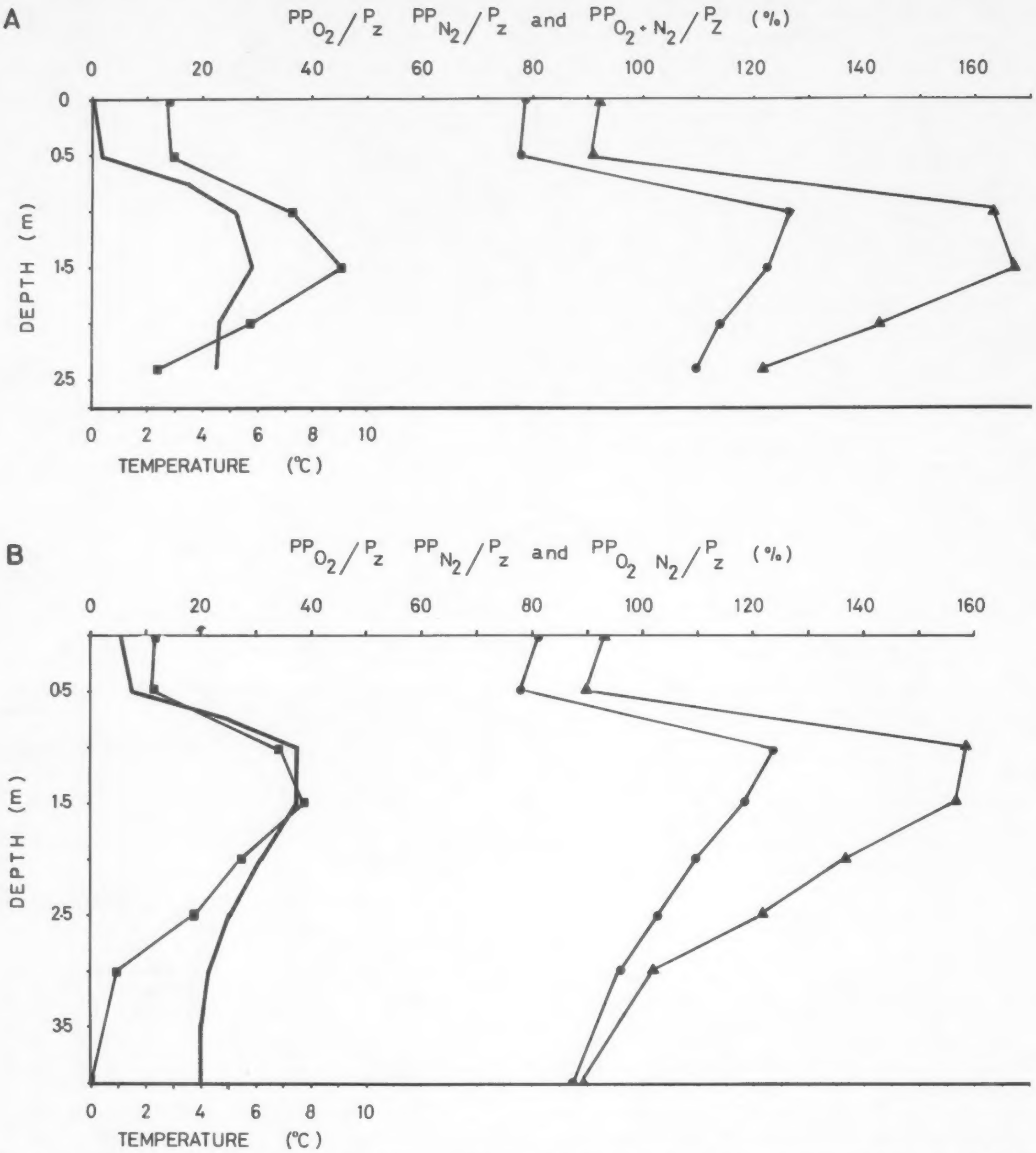

FIG. 5. 1977 depth distribution of the measured partial pressure of oxygen (■), the estimated partial pressure of nitrogen (●), and their sum, the total gas tension (▲), expressed as a percentage of the total hydrostatic pressure at depth. The depth distribution of temperature is shown for reference to the meltwater zone. (A) Lake 318; (B) lake 154; (C) lake 885. Lake 721 is not shown because oxygen concentrations were low.

squares from analysis of variance in regression) were as follows:

	r^2	F
% mortality vs nitrogen relative partial pressure	0.47	16.1
% mortality vs oxygen relative partial pressure	0.60	26.8
% mortality vs total relative partial pressure	0.71	43.5

Thus, total gas tension was a better predictor of trout mortality than the relative partial pressure of nitrogen or oxygen alone.

Discussion

Our observation that shallow lakes may become supersaturated with dissolved nitrogen during ice-cover is perhaps not

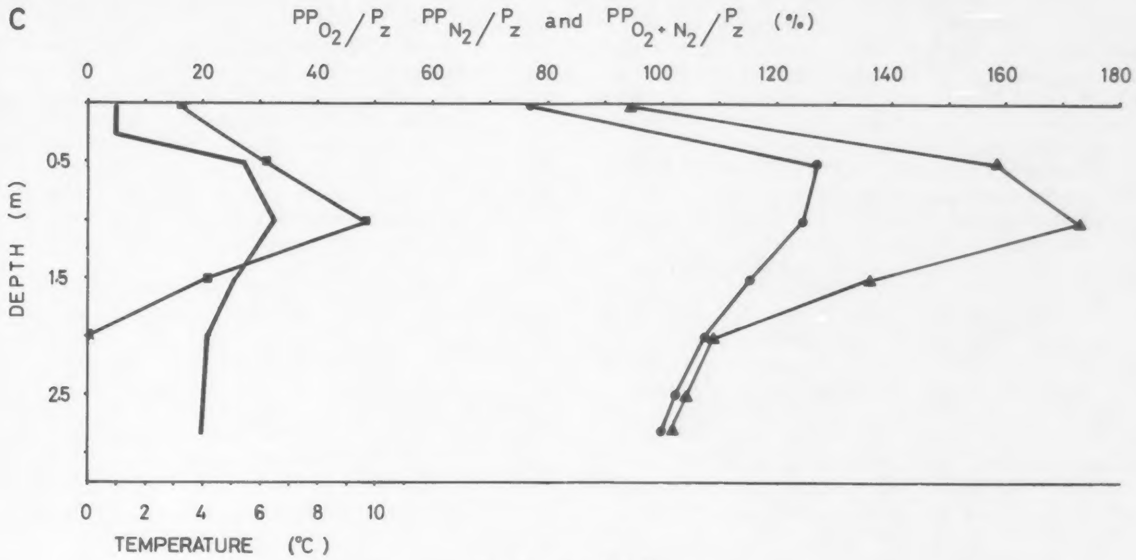

FIG. 5. (*Concluded*)

TABLE 5. Estimates of dissolved nitrogen concentrations beneath the spring ice in 1977.

	Lake		
	154	885	318
Water temperature at freeze-up, 1976 (°C)	1.4	2.0	2.0
N_2 solubility at 760 mmHg (mL/L)	18.25	17.97	17.97
Estimated dissolved N_2 concentration, fall 1976, at lake altitude (mg/L)	21.35	21.03	21.03
Maximum ice thickness, 1977 (m)	0.70	0.67	0.60
Lake volume at freeze-up (V_0)/ lake volume at maximum ice thickness (V_x)[a]	1.483	1.545	1.618
Predicted dissolved N_2 concentration under spring ice, 1977 (mg/L)	31.66	32.49	34.03
Applied to depths (m)[b]	1.0(+)	0.5(+)	1.0(+)

[a] See equation 3.

[b] At water depths shallower than those indicated, dissolved nitrogen concentrations were assumed to be at atmospheric equilibrium (see nitrogen freeze-out model under Results).

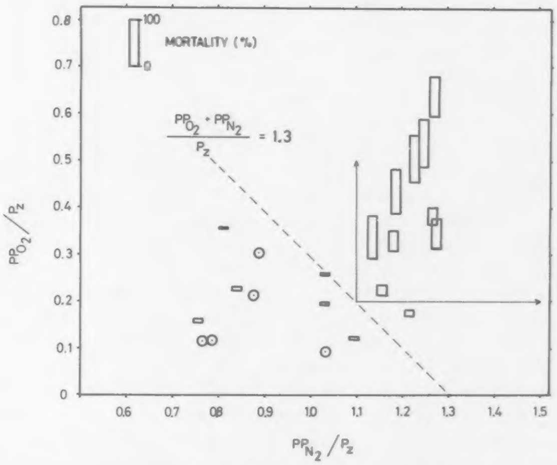

FIG. 6. Percent mortality of rainbow trout (vertical bars) as a function of the relative partial pressure of oxygen (ordinate) and nitrogen (abscissa). Circles represent zero mortality. Diagonal broken line represents the loci of all points where total gas tension equals 1.3 times the hydrostatic pressure.

surprising. The exclusion of solutes from lake ice is particularly important in shallow lakes where ice thickness is a large fraction of lake mean depth. Barica (1977) has shown that the increase in solute concentration is proportional to the decrease in lake volume resulting from ice formation. Dissolved gases behave in the same way as other solutes. Welch (1974) found that more than 97% of oxygen dissolved in the water column was excluded from the ice of an arctic lake, a result later corroborated for other arctic lakes (H. E. Welch, Freshwater Institute, Winnipeg, Man., pers. comm.). We suggest that the change in nitrogen concentration conforms to Barica's (1977) freeze-out hypothesis (Fig. 4), and may be calculated from measurements of ice thickness and the mean depth of a lake, neglecting the insignificant input of nitrogen through denitrification near the bottom during winter anoxia.

In much of the literature dealing with gas bubble disease in fish (i.e. Rucker 1972; Harvey 1967, 1975; Fickeisen and Schneider 1976), oxygen or nitrogen saturation is defined as the oxygen (nitrogen) concentration, expressed as a percentage of the oxygen concentration which would occur in surface water in equilibrium with the atmosphere. It is usually assumed that the water temperature is the same as that for the depth at which saturation is being expressed. This definition, however, is of limited use for a discussion of gas bubble disease in natural waters for two reasons. First, to a fish at depth, it is the tendency of bubbles to form in situ that is the measurement of concern. In considering bubble formation, gas saturation measures must be referenced to the solubility of the gas at the in situ hydrostatic pressure, rather than at atmospheric pressure (Miyake 1951). Second, gas bubble disease can occur "when the *total pressure of dissolved gases* (i.e. *the sum of their individual tensions*) greatly exceeds the hydrostatic pressure, including the pressure of the atmosphere" (Doudoroff 1957, emphasis ours). Therefore, any measure of percent gas saturation must also take into consideration the relative partial pressures of other gases in situ. In practice, only oxygen and nitrogen are usually considered, though methane may be important (Hutchinson 1957).

The absolute standard of oxygen saturation formulated by Ricker (1934) (equation 1, Methods) meets both of the above requirements. However, Ricker's formulation is only useful if the right-hand side of equation 1 is positive. When it is negative (i.e. nitrogen is already supersaturated with respect to total pressure), no useful information is obtained regarding the total gas tension or the relative contribution of the two gases in causing bubbles to form. We propose a more general expression of Ricker's formulation (see equation 2, Methods) which specifically indicates the relative partial pressures of each gas (with respect to the total hydrostatic pressure), as well as the total gas saturation as a proportion of total hydrostatic pressure. When the latter exceeds 1.0, bubbles would tend to form and there would be a potential for gas bubble disease to appear in fish. Our expression for the "relative partial pressure" of a gas, as in equation 2, is essentially similar to the term "saturation percentage *in situ*" as used by Miyake (1951) in calculating the formation of bubbles in the sea.

In water that is in equilibrium with the atmosphere, the relative partial pressure of dissolved oxygen and nitrogen is approximately 20 and 80%, respectively. Under the special conditions found in our study lakes, however, these relative partial pressures rose to 25–40% for oxygen and to greater than 120% for nitrogen (Fig. 5A–5C). The total relative gas saturation (i.e. the sum of the relative partial pressures of oxygen and nitrogen) exceeded 160%. The maximum total gas tension was associated with the uppermost part of the unmixed water mass where temperatures were highest and hydrostatic pressure was low. The decrease in relative partial pressure of oxygen below this point was due to increased hydrostatic pressure, cooler water, and lower oxygen concentrations. The dissolved nitrogen concentration did not vary consistently with depth through the unmixed water layer, so that changes in the relative partial pressure of nitrogen (Fig. 5) reflect only the effects of decreasing temperature and increasing pressure.

Our data (Fig. 6) suggest that acute gas bubble mortality results from a total gas tension about 130% greater than hydrostatic pressure. In our experiments these conditions were associated with relative partial pressures of nitrogen above 110% and of oxygen above 20%. Blahm et al. (1976) found that the time required for 50% of rainbow trout to succumb to bubble disease was 142 h at 120% nitrogen saturation and 47 h at 130% saturation. Similarly, Dawley et al. (1976), using nitrogen and argon to elevate gas tensions, found that 50-g rainbow trout began to experience significant mortality at 115% saturation in 0.25-m-deep tanks and at 127% saturation in 2.5-m-deep tanks (20% mortality after 7 d). Most gas bubble mortality in our experiment was observed between 1.0 and 2.0 m depth. Weitkamp (1976) held 105-mm Chinook salmon (*Oncorhynchus tshawytscha*) in cages at an elevated nitrogen partial pressure of 120–128% air saturation and found that 100% died after 3 d in 0- to 1-m cages, 75% died after 18 d in 0- to 3-m cages, and none died in 20 d in 0- to 4-m cages. Direct comparisons with our data are difficult because in many studies, gas supersaturation is not expressed in terms of hydrostatic pressure, and as shown by the studies cited above, mortality responses are pressure dependent. In addition, Dawley et al. (1976) have shown that there is an inverse relationship between the size of steelhead (rainbow trout) and the resistance time to gas bubble disease, so that fish size must also be standardized for direct comparison. Nevertheless, our field results with 10-g trout measured over 24 h appear consistent with laboratory studies.

The elevated nitrogen partial pressures that we recorded are probably the key to understanding trout mortality in this study, even though percent mortality was more highly correlated with oxygen relative partial pressure than with nitrogen. High relative partial pressures of oxygen did not result in gas bubble mortality in trout unless superimposed upon already high partial pressures of nitrogen (Fig. 6). Although elevated oxygen tension alone can cause gas bubble disease, the required oxygen content must be 300% of air saturation (Stickney 1968) or higher (Englehorn 1943) with no decrease in the nitrogen partial pressure. It is noteworthy in comparison that our empirical estimate of the relative gas tension required to cause 24-h mortality in rainbow trout (1.3 times the total hydrostatic pressure, as indicated by the broken line in Fig. 6) implies an oxygen content of about 250% of air saturation (relative partial pressure of oxygen approximately 0.2), when the nitrogen content is approximately at air saturation (relative partial pressure 0.8).

The biologically inert nature of dissolved nitrogen makes its contribution to total gas pressure more serious with respect to gas bubble disease than that of oxygen. Analysis of the gas in bubbles taken from the skin of brown trout (*Salmo trutta*) (Engelhorn 1943) has shown that oxygen is removed from the bubbles by the surrounding tissues, whereas nitrogen remains in excess. Rucker (1972) showed that at a constant total gas tension of 119%, the mortality rate of coho salmon (*Oncorhynchus kisutch*) fingerlings was much higher with nitrogen in excess than with oxygen in excess. Presumably, high oxygen tension in the blood is partially alleviated by the oxygen demand of the tissues.

Our results suggest that dissolved nitrogen can become supersaturated under ice in shallow lakes where ice thickness is a significant proportion (greater than about 15%) of lake mean depth. This condition is commonly observed in prairie lakes. Furthermore, because prairie lakes tend to be nutrient rich, primary production elevates dissolved oxygen concentrations to supersaturated levels, contributing to even higher gas tensions prior to the spring icemelt. Rainbow trout are unable to sense gas supersaturation (J. A. Mathias, in prep.), and if gas tensions are high enough, the fish succumb to gas bubble disease. The advantages of stocking fingerlings beneath the ice to minimize bird predation (Ayles et al. 1976) and take advantage of a longer growing season are therefore outweighed by the risks associated with gas bubble disease.

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Experimental and Field Evidence for Inter- and Intraspecific Competition in Two Freshwater Fishes[1]

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Hanson, J. M., and W. C. Leggett. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. Can. J. Fish. Aquat. Sci. 42: 280–286.

Direct evidence for intra- and interspecific competition in fishes was obtained by manipulating populations of yellow perch (*Perca flavescens*) and pumpkinseed (*Lepomis gibbosus*) stocked into littoral zone enclosures. Stocking densities were above, below, and equal to measured littoral zone fish biomass. There were no significant differences in mean percent weight change at given densities among repeated experiments (each of 14-d duration). In experiments testing for intraspecific competition, all fish reared at low density gained weight, all fish reared at high density lost weight, and mean weight change at natural density did not differ from 0.0. In experiments testing for interspecific competition, growth of pumpkinseed did not differ from growth of pumpkinseed reared alone at equivalent densities whereas growth of yellow perch was depressed relative to growth of yellow perch reared alone at equivalent densities. These growth changes did not result from behavioural interactions. We conclude that (a) inter- and intraspecific competition for food is significant at natural fish densities and (b) pumpkinseed are superior to perch when competing for food. A marked reduction in yellow perch growth in Lake Memphremagog between 1972 and 1983, coincident with a major increase in pumpkinseed abundance, is consistent with these findings and our interpretations.

Une manipulation de populations de perchaude (*Perca flavescens*) et de crapet-soleil (*Lepomis gibbosus*), peuplant des parcs ancrés dans une zone littorale, a fourni des preuves d'une compétition intraspécifique et interspécifique. Les densités déversées ont été supérieures, égales et inférieures à la biomasse ichtyocole quantifiée dans la zone littorale. Il n'y a pas eu de différence significative entre les variations du poids moyen en pourcentage à des densités connues entre les expériences (d'une durée de 14 jours chacune). Dans les expériences sur la compétition intraspécifique, tous les poissons élevés à de faibles densités ont pris du poids tandis que ceux gardés à de fortes densités en ont perdu. La variation du poids moyen à une densité normale ne s'est pas éloignée de 0,0. Pour ce qui est des expériences sur la compétition interspécifique, la croissance des crapets-soleils ne s'est pas distinguée de celle des individus élevés seuls, à des densités équivalentes, tandis que la croissance des perchaudes a été moindre par rapport à celle des individus élevés seuls, à des densités équivalentes. Ces variations de la croissance n'ont pas résulté d'interactions comportementales. Les auteurs concluent que (a) la compétition interspécifique et intraspécifique pour la nourriture est significative, à des densités naturelles, et (b) le crapet-soleil a plus de succès que la perchaude dans la compétition pour la nourriture. Une baisse prononcée de la croissance de la perchaude dans le lac Memphrémagog, de 1972 à 1983, coïncidant avec une augmentation importante de l'abondance du crapet-soleil, concorde avec les présentes données et leur interprétation.

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There is considerable interest, and controversy, over the role of competition in shaping plant and animal communities, and the absence of clear evidence for competition in many species assemblages plays no small role in this controversy (e.g. Roughgarden 1983; Quinn and Dunham 1983; Connor and Simberloff 1983; Simberloff 1983; Strong 1983). The potential for competition among selected groups of freshwater fishes is possibly greater than for other species assemblages because the geographical ranges of numerous freshwater fishes have expanded greatly in recent times (Lee et al. 1980) due to accidental or intentional species introductions (e.g. Smith 1972; Li and Moyle 1981; Gophen et al. 1983) and because the total biomass of fish in lakes is strongly coupled to nutrient levels and largely independent of species number (Hall et al. 1970; Boyd 1981; Hanson and Leggett 1982). Our recent empirical work showed that total fish biomass is also strongly correlated with macrobenthos biomass, again independent of species numbers (Hanson and Leggett 1982). These studies and others indicate that, globally, fish populations are food limited and the relative proportions of the various fish species in a given lake must, therefore, reflect the ongoing interactions between competitors and predators. We hypothesized that individual species expand their diet to include previous unexploited food types when interspecific competition is reduced, thereby maintaining a constant total fish biomass irrespective of species numbers (Hanson and Leggett 1982). The frequent observation that successful introduction of a new species into a lake causes a reduction of the total biomass of the original species assemblage (Stewart et al. 1981; Waters 1983; Inskip and Magnuson 1983; and others) is consistent with this hypothesis.

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[1] A contribution of the Lake Memphremagog Project, Limnology Research Center, McGill University.

Direct evidence for interspecific competition among freshwater fish is scarce and the results of studies to date are by no means clearcut. The purpose of this study was to test for competition between two species of freshwater fishes and to compare the relative strength and directionality of inter- and intraspecific competition.

Three methods have been used to study competition in freshwater fish communities. The niche overlap method assumes that some resource (usually food) is limiting and that sympatric species must segregate along some niche axis (e.g. Mendelson 1975; Marrin and Erman 1982; Gladfelter and Johnson 1983). This approach has been criticized because it is often unclear which resource, if any, is limiting (Mendelson 1975; Baker and Ross 1981; Van Der Avyle et al. 1983), because overlap indices are generally insensitive to changes in resource availability (Abrams 1980), and because the use of a method that assumes competition to detect competition is tautological (Hairston 1983). The occurrence of overlap in resource use between two species does, however, indicate that interspecific competition could occur.

The second method involves comparative studies of patterns of resource use (usually food) to detect niche shifts when species are sympatric and allopatric to potential competitors (e.g. Nilsson and Northcote 1981; Schmitt and Coyer 1983). It is, however, difficult to distinguish between the interacting effects of differing environments, predation, and the presence of competitors in these "natural experiments" (Sale 1979; Connell 1980; Schmitt and Coyer 1983).

Neither the measurement of diet overlap nor the detection of diet shifts between sympatric and allopatric species populations constitutes direct evidence for competition. Freshwater fish generally show considerable diet flexibility (Larkin 1956; Keast 1979; Dill 1983), and changes in diet and diet overlap frequently result from normal seasonal changes in prey abundance (Nilsson 1960; Keast 1977; Baker-Dittus 1978). Futhermore, a clear demonstration of competition requires that the changes in diet or diet overlap be accompanied by a reduction in fitness (such as decreased growth, fecundity, or survival) which is clearly attributable to the effects of two or more species on each other (Sale 1979; Connell 1983; MacNally 1983). To our knowledge, no such evidence exists.

The most direct, and most difficult, method of detecting competition is the carefully controlled field experiment (Hairston 1981; Schoener 1983; Connell 1983). This method has not been applied extensively to freshwater fish populations. Werner and Hall (1976, 1977, 1979) sought evidence for niche shifts among sunfish species (Centrarchidae) in small artificial ponds. The insights gained from these experiments are reduced by the unnaturally high densities of fish used, the absence of controls in two of the three experiments, and an inability to distinguish between food and space limitation because one species, the green sunfish (*Lepomis cyanellus*), is highly territorial (Greenberg 1947; Werner and Hall 1977). Clady (1981) observed diet shifts between largemouth bass (*Micropterus salmoides*) and spotted bass (*M. punctulatus*), again stocked at unnaturally high densities in an artificial pond. There were, however, no interspecific effects on growth or diet when the experiments were repeated at more natural densities (Clady and Luker 1982).

The limitations in these studies emphasize the need to conduct additional carefully controlled experiments to test directly for interspecific competition under natural conditions.

Materials and Methods

We tested for the existence and magnitude of competitive interactions between yellow perch (*Perca flavescens*) and pumpkinseed (*Lepomis gibbosus*) by experimentally manipulating the densities of yellow perch and pumpkinseed in enclosures installed in the littoral zone of MacPherson Bay (72°15′30″W; 45°06′30″N) in the central basin of Lake Memphremagog, Quebec–Vermont. The morphology and water chemistry of Lake Memphremagog have been described previously in Nakashima and Leggett (1975) and Nakashima et al. (1977).

Yellow perch and pumpkinseed commonly occur in the littoral zone of lakes and streams in eastern North America, and both have been introduced widely outside of their original geographical ranges (Lee et al. 1980). Yellow perch and pumpkinseed are potential competitors because age I and older yellow perch and pumpkinseed >20 mm (TL) prey extensively upon a wide range of aquatic insects, crustaceans, and molluscs in the littoral zone (Clady 1974; Nakashima and Leggett 1975; Keast 1977, 1978a; Beaulieu et al.1979; Hanson and Qadri 1984).

Our measure of competition was changes in growth rates in experimental versus control enclosures. We also sought corroborative field evidence of competition between yellow perch and pumpkinseed by comparing growth of yellow perch in Lake Memphremagog in 1972–73 (Nakashima and Leggett 1975) when pumpkinseed were rare (Gascon and Leggett 1977) with growth of yellow perch in 1983 when pumpkinseed numbers had increased to the point where they were the second most abundant littoral zone species. Water quality and nutrient levels in 1982 (Pace 1984) have not changed compared with earlier years.

Littoral Zone Fish Biomass

To establish appropriate stocking densities we quantitatively sampled littoral zone fishes >30 mm in length with a 50 × 3 m bag seine (6-mm knotless mesh) which was dyed green and brown. The seine was deployed to enclose an area of 400–600 m^2 varying in depth from 0.5 to 3.0 m. The fish catch was sorted to species and the total biomass (blotted wet weight) of each species was determined to an accuracy of 0.1 g.

The sampling efficiency of the seine was assessed by a diver who followed the seine during eight net hauls. Fish escaped from the net only when it became snagged on rocks or logs; all such samples were excluded from our analysis. Seine efficiency was also tested in an area of greater macrophyte abundance located in Newport Bay at the southern tip of Lake Memphremagog. There, 96 and 100% of two groups of marked fish introduced into the deployed seine were recaptured (Boisclair 1984).

In total, 20 successful seine samples were obtained from seven sites within the central basin of Lake Memphremagog. Sixteen of the samples were taken from July to early September 1981, and an additional four samples were taken at the end of August 1982.

Experimental Enclosures

Seven enclosures (4.8 × 4.8 × 1.8 m) were placed in a single line parallel to shore in a small cove in MacPherson Bay. The water depth in each enclosure was about 0.7 m near shore and 1.4 m at the side furthest from shore. The substrate was soft muck with woody debris and leaf detritus. The common macrophytes, which were not abundant, were *Vallisneria americana*, *Potamogeton crispus*, *Najas flexilis*, *Myriophyllum spicatum*, and *Chara* spp.

The frames of the enclosures were constructed of 5 × 10 cm lumber. A 30 × 2 cm plywood baseboard was attached to the lower border to allow the enclosures to be sunk into the sediments. Each enclosure was lined with 1.3-mm-mesh fiberglass window screening and covered on the outside with chicken wire. About 70 cm of chicken wire was attached to the plywood baseboard of the enclosure, sunk into the substrate, covered with 10–15 cm of gravel, and then covered with rocks. These extraordinary precautions were necessary to prevent brown bullhead (*Ictalurus nebulosus*) from excavating nesting burrows under the sides of the enclosures and to prevent storm-induced wave action from washing holes under the sides of the enclosure. Avian predation was eliminated by suspending two 1.4-m-wide sections of window screening across the top of each enclosure and then suspending two 2-m-wide sections of gill net perpendicular to the screen.

Experimental Procedures

Enclosures were installed between June 16 and 18, 1983, and allowed to stabilize for 1 wk. Experimental populations consisted of single species assemblages of 150 g (low density), 300 g (natural density), or 600 g (high density) of yellow perch or pumpkinseed and one mixed assemblage of 150 g each of yellow perch and pumpkinseed. The 300-g stocking level corresponded to the measured average total fish biomass on the littoral zone in the study area. Each experimental population was assigned initially to an enclosure at random. In subsequent experiments the same assignment of species assemblages to specific enclosures was maintained. Due to space and time limitations, only one replicate of each treatment was possible for each experiment.

All fish used in the experiments were caught by seining in the central basin of Lake Memphremagog. Following capture they were transported to our lakeside laboratory at MacPherson Bay in large, waterfilled styrofoam containers. There they were weighed (blotted wet weight ± 0.05 g), individually marked near the dorsal fin by an intramuscular injection of acrylic paint, and stocked into the appropriate enclosure. The actual stocking biomasses, stocking schedule, number of fish stocked, and size range used are provided in Table 1. The range of fish sizes was chosen to ensure that the full size range of benthic prey present (determined a priori) could be consumed by the fish. To the maximum extent possible, each experimental population contained the full size range of fish.

All experiments were of 14-d duration. Enclosure integrity was checked daily. In addition, the fish in the enclosures were observed for about 2 h daily to check for possible agonistic behaviour, infection, and mortality. On the morning of day 15 the screens and gill nets were removed from the enclosures by 08:30. All fish were removed with a small seine, killed with 2-phenoxyethanol to prevent stomach content regurgitation, placed in labelled plastic bags, and stored in ice. Complete removal of fish from the seven enclosures took less than 90 min. Individual fish were identified, weighed, and the percent change in weight of each fish was calculated. The stomach and intestinal contents of each fish were removed, placed in separate labelled 25-mL vials, and stored in 2% formaldehyde for later analysis.

TABLE 1. Schedule of experiments designed to test for inter- and intraspecific competition. PS = pumpkinseed; YP = yellow perch. Mortality refers to unexplained mortality.

Treatment (g)	Species	No. of fish	Weight range (g)	Mortality (no.)
	Stocking date: July 12		*Recovery date: July 27*	
(1) 607.6	YP	27	6.1–34.5	8
(2) 609.2	PS	31	6.7–31.7	8
(3) 318.8	YP	16	5.4–29.0	1
(4) 298.0	PS	17	6.2–23.6	1
(5) 160.1	YP	14	5.1–20.3	0
(6) 158.7	PS	15	5.1–24.7	1
(7) 153.8	YP	12	6.2–23.6	1
155.8	PS	13	5.1–24.3	0
	Stocking date: July 28		*Recovery date: August 11*	
(1) 602.5	YP	28	5.7–30.0	6
(2) 603.9	PS	36	5.7–29.3	3
(3) 307.5	YP	16	6.3–29.7	1
(4) 302.3	PS	17	5.2–25.6	2
(5) 153.1	YP	12	5.8–27.0	0
(6) 154.0	PS	15	6.0–22.7	1
(7) 158.8	YP	13	7.5–21.8	0
152.7	PS	15	5.3–21.3	1
	Stocking date: August 14		*Recovery date: August 29*	
(1) 616.5	YP	44	5.7–32.1	8
(2) 602.1	PS	33	5.8–28.7	9
(3) 299.8	YP	18	6.3–30.9	1
(4) 314.0	PS	24	5.2–24.5	0
(5) 150.8	YP	13	6.0–29.7	0
(6) 157.8	PS	14	7.7–20.0	1
(7) 158.8	YP	12	5.5–30.7	1
150.3	PS	14	6.7–13.8	1

In Situ Growth of Yellow Perch

To determine whether there was any correlation between growth rates of yellow perch and the increase in the pumpkinseed population which had occurred in Lake Memphremagog between 1973 and 1983 we sampled yellow perch in MacPherson Bay during the last week of May and the first week of June 1983 by seining and gillnetting. The timing of this sampling corresponded with the sampling period used by Nakashima and Leggett (1980) to estimate yellow perch growth in 1972–73. Each fish was measured to the nearest mm (FL), weighed (blotted wet weight ± 0.05 g), and a sample of 20–30 scales were taken from near the tip of the left pectoral fin. A total of 183 yellow perch were successfully aged using the methods of Nakashima and Leggett (1975). A further sample of 41 fish were caught by seining on October 7, 1983, to verify scale aging through comparison with otolith-derived age (Beamish and McFarlane 1983). Only 2 of 41 scale/otolith ages differed. For these fish the age as determined from scales was 5+ yr whereas that determined from otoliths was 6+.

Statistical analysis of the data was performed using the SAS statistical package. Data were transformed, where required, to stabilize the variance.

Results

Littoral Zone Fish Biomass

The mean (±95% CI) fish biomass for the total littoral fish community was 12.6 ± 2.08 g/m^2. A total of 16 species was regularly captured (Table 2). Yellow perch and pumkinseed comprised 34 and 27% of the biomass, respectively. No other species constituted more than 8% of the total biomass in the samples.

Mortality

The screens and nets on the enclosures were effective in eliminating predation by belted kingfisher (*Megaceryle alycon*) and great blue heron (*Ardea herodias*). Eleven fish were, however, lost to kingfisher predation when the screens and nets were removed to enable seining of the enclosures. The enclosure with the natural density of pumpkinseed was particularly susceptible (six fish in total) because it lay under an electrical wire which was used frequently as a perch by the kingfishers. The only other known source of mortality was a severe storm on August 10 which killed eight fish, one or two per enclosure. Both sources of mortality occurred after effects of treatment upon growth had occurred. Unexplained mortality was 0–2 fish (mean 3.2%, range 0–11%) in the low and natural density enclosures and 3–8 fish (mean 20.5%, range 8–27%) in the high density enclosures (Table 1).

The experiment begun on June 27 and terminated on July 11 was omitted from the analysis because over 50% of the yellow perch in the natural and high density enclosures developed large necrotic lesions and died during the last week of the experiment. While we avoided using fish exhibiting white patches, open sores, or fungus in stocking our enclosures, we noted that about 25% of yellow perch collected by seining on June 27 had these symptoms. With the exception of this experiment there was no evidence of infection or disease in the experimental animals prior to or during the experiments.

TABLE 2. Biomass estimates (g/m^2, wet weight) of commonly captured fish species in the littoral zone of the central basin of Lake Memphremagog during 1981 (mean of 20 samples; average total biomass (±95% CI) = 12.6 ± 2.08 g/m^2).

Species	Mean	±95% CI	% total biomass[a]
Perca flavescens	4.26	0.988	33.6
Lepomis gibbosus	3.37	1.737	26.6
Ambloplites rupestris	0.94	0.631	7.4
Micropterus dolomieui	0.50	0.459	4.0
Micropterus salmoides	0.14	0.157	1.1
Esox niger	0.65	0.268	5.2
Ictalurus nebulosus	0.47	0.398	3.7
Catostomus commersoni	0.79	0.273	6.3
Notropis volucellus	0.55	0.481	4.3
Notemigonus crysoleucas	0.52	0.219	4.1
Pimephales notatus	0.25	0.205	2.0

[a] The remaining 1.7% consisted of *Etheostoma olmstedi* (misidentified as *E. nigrum* by Gascon and Leggett 1977), *Notropis cornutus*, *N. rubellus*, *N. bifrenatus*, and *Hybognathus nuchalis*.

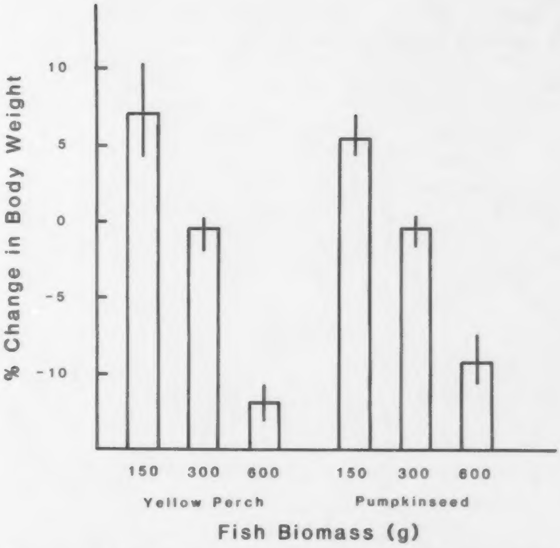

FIG. 1. Average growth of yellow perch and pumpkinseed in enclosures (intraspecific competition). Results of three experiments are pooled because no between experiment differences in growth occurred. Means ± 95% CI of the pooled data are presented.

Competition Experiments

Both yellow perch and pumpkinseed showed significant reductions in growth in response to increased biomass when held in single species assemblages (Fig. 1). There were no significant differences between repetitions in time (Table 3). All fish in the low density enclosures gained weight and all fish in the high density enclosure lost weight (despite the higher mortality). Average growth at the natural biomass level was not significantly different from 0.0 (*t*-test, $P > 0.05$). No intraspecific agonistic behaviour was observed. Feeding occurred primarily in the morning hours following daybreak.

Yellow perch and pumpkinseed differed in their response to addition of the second species (Fig. 2). There were, again, no significant differences between repetitions in time (Table 4). Both species exhibited a decrease in growth rate when the second species was added. The decrease in pumpkinseed growth due to the addition of perch was equivalent to the addition of an equivalent biomass of pumpkinseed in the single species experiments. The decline in perch growth following the addition of pumpkinseed was significantly greater than the growth reduction observed when an equivalent biomass of yellow perch was added in single species experiments. The results indicate that competition occurred between yellow perch and pumpkinseed, and that this competition was asymmetrical. Pumpkinseed were superior competitors under these experimental conditions. These differences were not due to interspecific agonistic behaviour. We observed no such behaviour and, in fact, yellow perch and pumpkinseed were frequently observed feeding together in the same group.

In Situ Growth of Yellow Perch

Overall, the fork lengths of 1- to 7-yr-old yellow perch sampled from Lake Memphremagog in 1983 were significantly less than the fork lengths of like-aged yellow perch sampled in 1972–73 (Fig. 3; Wilcoxon signed-rank test, $P = 0.031$). This

TABLE 3. ANOVA for effects of fish biomass and time (replicate experiments) on mean % change in weight of yellow perch and pumpkinseed (D_1 = 150 g/enclosure; D_2 = 300 g/enclosure; D_3 = 600 g/enclosure; NS = not significant).

Source of variation	df	Sum of squares	*F*	*P*
		Yellow perch		
Density	2	1825.6	85.60	<0.005
Time	2	95.1	4.66	NS
D_1 vs D_2, D_3	1	1417.2	138.86	<0.005
D_2 vs D_3	1	408.4	40.01	<0.005
Error	4	40.8		
		Pumpkinseed		
Density	2	1433.7	217.04	<0.005
Time	2	11.7	1.77	NS
D_1 vs D_2, D_3	1	1179.8	357.20	<0.005
D_2 vs D_3	1	253.9	76.87	<0.005
Error	4	13.2		

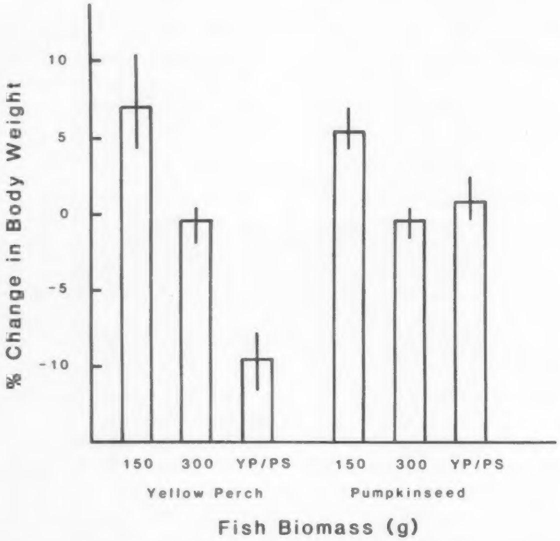

FIG. 2. Average growth of yellow perch and pumpkinseed in enclosures (interspecific competition). YP/PS = 150 g yellow perch + 150 g pumpkinseed. Results of three experiments are pooled because no between experiment differences in growth occurred. Means ± 95% CI of the pooled data are presented.

TABLE 4. ANOVA for effects of fish biomass and time (replicate experiments) on mean % change in weight of yellow perch and pumpkinseed (D_1 = 150 g/enclosure of yellow perch or pumpkinseed; D_2 = 300 g/enclosure of yellow perch or pumpkinseed; D_3 = 150 g of yellow perch and 150 g of pumpkinseed/enclosure; NS = not significant).

Source of variation	df	Sum of squares	*F*	*P*
		Yellow perch		
Density	2	1655.8	92.71	<0.005
Time	2	93.1	5.21	NS
D_1 vs D_2, D_3	1	1327.5	148.66	<0.005
D_2 vs D_3	1	328.3	36.76	<0.005
Error	4	35.7		
		Pumpkinseed		
Density	2	475.0	10.42	<0.025
Time	2	36.3	0.80	NS
D_1 vs D_2, D_3	1	340.9	14.95	<0.025
D_2 vs D_3	1	133.1	5.88	NS
Error	4	91.2		

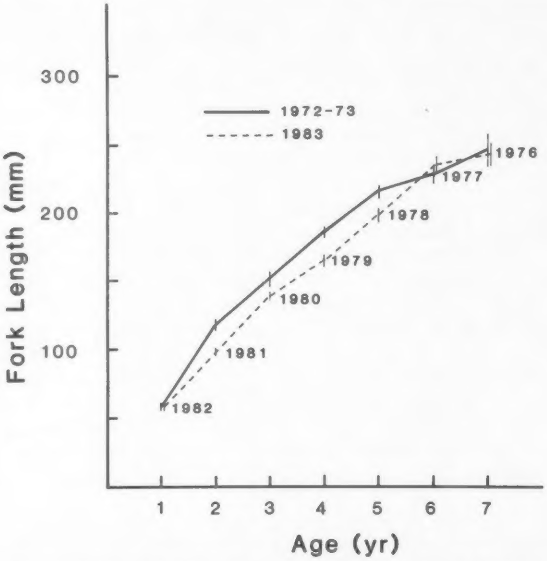

FIG. 3. Average fork length at age for yellow perch collected in the central basin of Lake Memphremagog in 1972–73 and 1983. Means ± 95% CI are presented. Dates represent year of birth for yellow perch alive in 1983.

reduced growth appears to occur in the second summer of life because fishes aged 2–5 yr were 20 mm smaller in 1983 than in 1972–73 whereas fishes aged 1+ yr were identical in length in both years. This decrease in the growth rate of yellow perch corresponds to the period during which the biomass of pumpkinseed sunfish increased several-fold in Lake Memphremagog. It is also consistent with the results of our experiments which show that pumpkinseed sunfish are competitively superior to yellow perch when they occur together.

Discussion

This study provides clear evidence for intraspecific competition for food in freshwater fish populations. In our experiments, yellow perch and pumpkinseed showed identical responses to changes in biomass when held as single species assemblages: fish at low densities gained weight, fish at high densities lost weight, and fish at natural densities showed no net growth. These results and the absence of agonistic behaviour clearly demonstrate that both species experienced similar food limitation when stocked at comparable biomass. The absence of growth in both species when stocked at biomass levels equivalent to the mean total fish biomass on the littoral zone near the study site is consistent with empirical evidence that total fish biomass is strongly coupled to macrobenthic biomass and is independent of species number (Hanson and Leggett 1982). Under natural conditions the combined increase in biomass of individual fish during the growing season should be balanced by losses of biomass due to mortality. In the absence of significant mortality, growth should be negligible, as we observed. The frequently reported observation that growth in stunted fish populations improves following naturally or artificially induced increases in mortality, by introduction of predators (Tucker 1973; Svardson 1976; Forsythe and Wrenn 1979) or removal of a large part of the population by fishing (Cooper et al. 1971; Hanson et al. 1983), is also consistent with this interpretation.

Our in situ experiments provide direct evidence for interspecific competition among freshwater fishes by demonstrating that both yellow perch and pumpkinseed have a significant depressing effect on the growth of each other when competing for food. This competition was strikingly asymmetrical. The effects of intra- and interspecific competition were equal for pumpkinseed. Decreases in pumpkinseed growth following addition of yellow perch were exactly equivalent to reductions in growth following the addition of an equal biomass of pumpkinseed. For yellow perch, however, interspecific competition was stronger than intraspecific competition. The addition of a given biomass of pumpkinseed resulted in a significantly greater decrease in growth than the addition of an equivalent biomass of yellow perch.

The competition between yellow perch and pumpkinseed appears to be of the exploitative type because no agonistic behaviour was observed. We have examined the gut contents of yellow perch and pumpkinseed from our experiments for evidence of a diet shift (J. M. Hanson and W. C. Leggett, in prep.). When raised alone, the major prey types of both fish species were macroinvertebrates (amphipods, insect larvae, and gastropods). When reared together the pumpkinseed maintained a diet of macroinvertebrates whereas 30–52% (by weight) of the diet of yellow perch consisted of microcrustaceans. This diet shift is consistent with the hypothesis of competition for food.

Our experiments suggest that competition can have important effects even over short periods because we obtained significant and assymetrical competitive effects on growth in experiments of short duration. Connell (1983) has suggested that where strong asymmetrical competition persists the inferior competitor should be eliminated. This result is unlikely because predation (Glasser 1979; Connell 1983; Wilbur et al. 1983) and environmental variability (Wiens 1977; Moyle and Li 1979; Clady and Luker 1982) are known to moderate the intensity and effect of competition. This moderation would explain the fact that yellow perch and pumpkinseed regularly occur together in lakes (Werner et al. 1977; Keast 1978b; Fish and Savitz 1983).

Perturbation of the fish community through removal of predators and/or potential competitors by fishing, or through introduction of a superior competitor, can result in intensification of competition. Pumpkinseed have been introduced recently into Lake Memphremagog, although the exact date of introduction is unknown. The significantly reduced growth of yellow perch sampled in Lake Memphremagog in 1983 compared with fish sampled in 1972–73 coincides with a known increase in the biomass of pumpkinseed in the lake and is consistent with the results of our experiments which show pumpkinseed to be superior competitors. The result of this growth study suggests that the effect of this competition was most intense between age 1 and 2 because there was no significant difference in the size of age 1 yellow perch sampled in 1983 and 1972–73 (Fig. 3) whereas yellow perch aged 2–5 yr were, on average, 20 mm smaller in 1983. If competition were equally intense for all size or age groups the difference in fork lengths at each age should increase with age. Yellow perch aged 6 and 7 yr were the same length in 1983 and 1972–73. These 1983 fish were spawned in 1977 and 1976, respectively. It is possible that the pumpkinseed population, which was small in 1974 (Gascon and Leggett 1977), had not expanded sufficiently to affect yellow perch growth by 1976 or 1977. Further work is required to test directly whether the competitive effect of pumpkinseed on yellow perch is most intense at age 1, when yellow perch change their diet from zooplankton to macrobenthos (Clady 1974; Nakashima and Leggett 1975; Keast 1977). We did not partition our experiments into different size classes of yellow perch or pumpkinseed and hence cannot resolve this question.

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Initial Egg Weight, Time to Maximum Alevin Wet Weight, and Optimal Ponding Times for Chinook Salmon (*Oncorhynchus tshawytscha*)

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Rombough, P. J. 1985. Initial egg weight, time to maximum alevin wet weight, and optimal ponding times for chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 42: 287–291.

Eggs of chinook salmon (*Oncorhynchus tshawytscha*) were segregated into eight size groups (range 163–437 mg) and incubated at 5, 7.5, 10, and 12.5°C. The time required to reach maximum alevin wet weight (MAWW) varied significantly ($p < 0.01$) both with mean incubation temperature (T °C) and with initial egg weight (W mg). A good ($R^2 = 98.4\%$, $n = 21$) prediction of days postfertilization to MAWW (D) is given by

$$\ln D = 5.88 - 0.152T + 0.000513W.$$

Optimal ponding times are closely associated with the attainment of MAWW and can be estimated using this equation. Data relating mean incubation temperatures (T) to actual ponding time were collected from 17 hatcheries throughout British Columbia. The equation

$$\ln D' = 5.99 - 0.150T,$$

where D' is days postfertilization to ponding, provided the best fit to the data ($R^2 = 97.5\%$, $n = 85$). Hatchery ponding times were not significantly different from times to MAWW predicted for 200-mg eggs.

Des œufs de saumon quinnat (*Oncorhynchus tshawytscha*) ont été divisés en huit groupes de poids (allant de 163 à 437 mg) et incubés à 5, 7,5, 10 et 12,5°C. Le temps nécessaire pour atteindre le poids humide maximale chez l'alevin (PHMA) a varié de façon significative ($p < 0{,}01$) en fonction de la température moyenne d'incubation (T °C) et du poids initial des œufs (P mg). L'équation suivante :

$$\ln D = 5{,}88 - 0{,}152T + 0{,}000513P.$$

fournit une bonne prédiction ($R^2 = 98{,}4\ \%$, $n = 21$) du nombre de jours (D) nécessaires pour obtenir le PHMA post-fertilisation. Le moment optimal du déversement en étang est étroitement lié à l'atteinte du PHMA et peut être déterminé à l'aide de cette équation. Des données mettant en corrélation la température moyenne d'incubation (T) et le moment réel du déversement en étang ont été recueillies à 17 piscifactures de la Colombie-Britannique. L'équation suivante :

$$\ln D' = 5{,}99 - 0{,}150T,$$

où D' est le nombre de jours post-fertilisation avant le déversement, a fourni le meilleur ajustement ($R^2 = 97{,}5\ \%$, $n = 85$). Les temps avant le déversement n'étaient pas significativement différents des temps jusqu'à l'obtention du PHMA prédits pour des œufs de 200 mg.

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There is some controversy among fish culturists as to the optimum time to initiate feeding of chinook salmon (*Oncorhynchus tshawytscha*). Heming et al. (1982) introduced chinook alevins to food at various times during yolk absorption and developed an empirical model relating the optimum time to initiate food presentation to incubation temperature. However, their recommended ponding times do not agree with the ponding times that experienced hatchery managers have discovered by trial and error to result in the best growth and survival. For example, Heming et al. (1982) recommended that feeding be initiated about 9 d later at 10°C and about 31 d later at 5°C than is current hatchery practice.

The optimum time to begin feeding chinook in the laboratory is closely associated with the attainment of maximum alevin wet weight (Heming et al. 1982). Smith (1958) reported that in rainbow trout (*Salmo gairdneri*) the period required to reach maximum alevin weight appeared to be dependent on initial egg size. Egg size is highly variable in chinook: it is not uncommon to find more than a threefold difference in the initial weight of eggs from the same population. Heming et al. (1982) used very large eggs in their experiments, and it seems likely that at least part of the discrepancy between their predicted ponding times and those actually used by hatchery managers can be attributed to differences in initial egg weight. In the current study, I examine the influence of initial egg size on the time required to reach maximum alevin wet weight, and by implication, on the optimum time to initiated feeding of chinook salmon.

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Materials and Methods

Gametes of chinook salmon were obtained from fish returning to spawn in the Big Qualicum River, Vancouver Island, B.C. Eight groups of eggs, with mean wet weights (±SD; $n = 30$) of 163 ± 7, 235 ± 10, 281 ± 9, 340 ± 9, 341 ± 36, 384 ± 27, 425 ± 11, and 437 ± 8 mg after water hardening were selected for experimental purposes. Eggs of the 163-, 235-, 281-, 340-, 425-, and 437-mg groups were obtained from individual females. Eggs were pooled from two females for the 384-mg group and from an unknown number of females (two ?) for the 341-mg group.

Eggs were fertilized by the dry method. The pooled milt of four males was used for the 163-, 281-, 340-, and 425-mg groups and the pooled milt of eight males for the 235-, 281-, 341-, and 437-mg groups. The fertilized eggs were placed in vertically stacked incubation trays (Heath Tecna Corp.) at densities of about 2000 eggs per tray. Tray position was assigned at random. Nominal water temperatures of 5.0, 7.5, 10.0, and 12.5°C were selected for incubation. All eight egg sizes were incubated at 10.0°C, 235-, 341-, and 437-mg eggs were incubated at 7.5 and 12.5°C, and 340-mg eggs were incubated at 5.0°C. Water temperatures were determined four times a day and averaged over the total incubation period (Table 1). Water flows were maintained at 12 L/min using filtered, dechlorinated water from the Nanaimo municipal supply (total hardness 12 mg/L as $CaCO_3$). Dissolved oxygen levels were measured periodically and always exceeded 90% of air saturation. Alevins were not fed during experiments.

Samples of 10 alevins were taken from each of the various size and temperature combinations at evenly spaced intervals between hatching and complete yolk absorption. Sample intervals ranged from 12 d at 5°C to 4 d at 12.5°C. Alevins were fixed in 5% neutral formalin for at least 21 d and then gently blotted dry and weighed to the nearest 0.1 mg. Fork lengths were measured to the nearest 0.5 mm. The yolk was dissected from the alevin and both the yolk and the remaining tissue were weighed to the nearest 0.1 mg.

Relationships between total alevin wet weight and time were estimated by fitting the data for each experimental group to a polynomial of the type $y = a + bx + cx^2 + dx^3 + e$, where y is total alevin wet weight and x is time postfertilization. Maximum alevin wet weights (MAWW) and times to MAWW were determined by taking the first derivative of the various equations and solving for the maximum.

Developmental indices (K_D) were calculated as

$$K_D = \frac{10(\mathrm{AWW})^{\frac{1}{3}}}{\mathrm{AFL}}$$

where AWW is total alevin wet weight (milligrams) and AFL is alevin fork length (millimetres) (Bams 1970). Values of K_D at MAWW were estimated for each experimental group by fitting the K_D values at the three sample periods immediately before and the three sample periods immediately after MAWW to a hyperbola of the type $K_D = a - b \ln t$, where t is days postfertilization, and then solving K_D using the predicted time to MAWW for t.

Percent embryonic tissue (P_T) was calculated by dividing tissue (alevin without yolk) wet weight by total alevin wet weight (Heming 1982). Values of P_T at MAWW were estimated for each experimental group by fitting the P_T values at the three sample periods immediately before and the three sample periods immediately after MAWW to a hyperbola of the type $P_T = a + b \ln t$ and then solving for P_T using the predicted time to MAWW for t. Percent yolk at MAWW can be obtained by subtracting values for P_T from 100.

Polynomial and multiple regressions were determined using Minitab computer programs (Ryan et al. 1976). Values for MAWW and time to MAWW, K_D, and P_T were subjected to analysis of variance and Duncan's multiple range tests. Values presented by Heming (1982) were included in the analyses.

I also assembled data relating mean incubation temperature to ponding time for chinook alevins reared at 17 hatcheries throughout British Columbia. The data were fitted to semilogarithmic, modified thermal sums, Beleradek and log-inverse Belehradek models as given in Alderdice and Velsen (1978) using a nonlinear parameter estimation procedure (Schnute 1982).

Results

Total alevin wet weight increases to a maximum well before the exhaustion of yolk reserves and then declines (Fig. 1). The crests of curves of alevin wet weight versus time are broad and it is difficult to obtain reliable estimates of times to MAWW by visual inspection because of the variability in alevin weight and the limited number of sample periods. This is especially true for alevins from pooled eggs (e.g. 384-mg group, Fig. 1). Estimating times to MAWW from polynomial regressions avoids this difficulty. Regressions were highly significant ($p <$

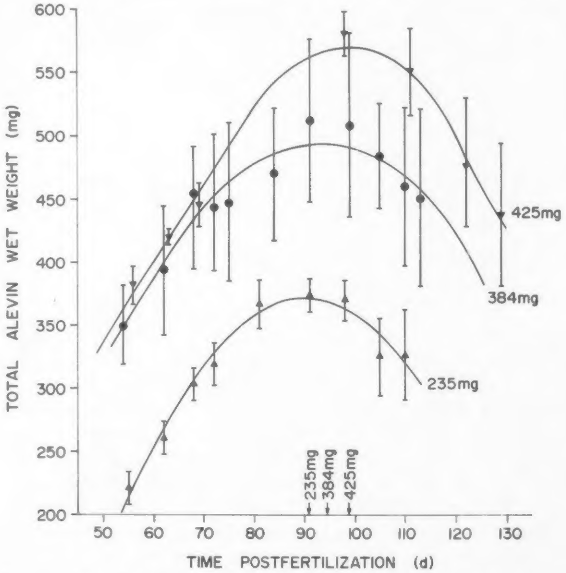

FIG. 1. Growth of chinook alevins from various size eggs at 10°C. Mean alevin wet weights (±95% CL; $n = 10$) and fitted polynomial curves are shown. Eggs with mean weights of 425 and 235 mg were obtained from single females. Eggs were pooled from two females for the 384-mg group. Arrows indicate the predicted time to MAWW for the various egg sizes.

TABLE 1. Mean temperature, initial egg weight, time to MAWW, accumulated thermal units (ATU, °C·d), MAWW, K_D at MAWW, and P_T at MAWW for chinook salmon.

Mean temperature (°C)	Initial egg weight (mg)	Time to MAWW (d)	ATU to MAWW	MAWW (mg)	K_D at MAWW	P_T at MAWW
5.0	340	200.5	1000	514	2.09	95.6
7.3	235	135.9	995	375	2.09	94.6
7.3	341	136.9	1002	542	2.17	93.8
7.3	384	142.3	1042	552	2.13	91.3
7.3	437	143.3	1049	634	2.18	89.0
10.0	163	84.3	860	245	2.06	88.4
10.2	235	90.8	926	372	2.13	89.4
10.0	281	89.8	896	371	2.14	83.6
10.2	340	95.7	955	458	2.20	81.0
10.2	341	88.3	901	482	2.22	81.2
10.2	384	94.5	964	493	2.16	86.6
10.0	425	98.7	985	567	2.20	88.5
10.2	437	94.5	964	580	2.21	83.9
12.5	235	64.8	813	343	2.23	81.8
12.5	341	58.4	732	408	2.45	66.1
12.5	384	64.9	814	463	2.33	72.9
12.5	425	62.2	780	512	2.42	65.8
5.9[a]	490	190	1121	663	2.15	—
7.9[a]	490	141	1114	642	2.17	—
9.8[a]	490	107	1049	616	2.19	—
11.8[a]	490	85	1003	594	2.24	—

[a] Heming (1982).

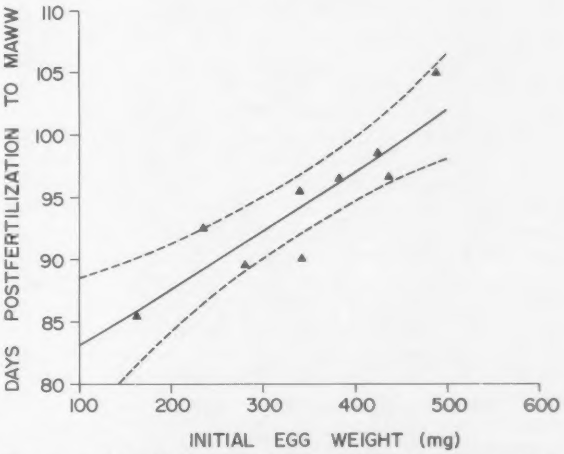

FIG. 2. Relationship between initial egg weight and the time required for chinook alevins to reach maximum wet weight at 10°C. Actual times to MAWW and the predicted curve, ln $D = 4.37 + 0.000507W$, and its 95% confidence limits are plotted.

0.01) for all groups and in most instances accounted for >90% of the variability in the data.

Estimated times to MAWW varied inversely with temperature and ranged from 200.5 d at 5°C (340-mg eggs) to 58.4 d at 12.5°C (341-mg eggs) (Table 1). Analysis of variance indicated that both temperature and initial egg weight significantly ($p < 0.01$) affected time to MAWW. The semilogarithmic relationship

(1) $\ln D = 5.88 - 0.152T + 0.000513W,$

where D is number of days postfertilization to MAWW, T is mean incubation temperature (°C) (degrees Celsius), and W is mean initial water hardened egg weight (milligrams), explained 98.4% of the variability in the data ($n = 21$), with incubation temperature accounting for 96.4%. Although initial egg size accounted for only 2.0% of the overall variability, it did have a highly significant ($p < 0.01$) effect on time to MAWW at a given temperature. This is best illustrated using the 10°C data (Fig. 2) where the relationship between time to MAWW and initial egg size is described by

(2) $\ln D = 4.37 + 0.000507W \quad (R^2 = 79.9\%;\ n = 9).$

The maximum weight attained by alevins also was significantly ($p < 0.01$) affected by both initial egg weight and temperature. The regression

(3) $\mathrm{MAWW} = 241 + 1.07W - 14.3T$

explained 96.4% of the variability in the data ($n = 21$). As expected, initial egg weight accounted for most of the variability (88.4%).

Developmental indices varied inversely with incubation period and temperature and directly with initial egg weight. The equation

(4) $K_D = 9.60 - 1.34 \ln d - 0.168T + 0.0011W,$

where d is the number of days postfertilization, accounted for 89.2% of the variability in the data ($n = 154$). Developmental indices at MAWW can be predicted from the pooled data by substituting equation (1) for ln d in equation (4) to yield

(5) K_D at $\mathrm{MAWW} = 1.72 + 0.036T + 0.000413W.$

Actual K_D values at MAWW ranged from 2.06 for 163-mg eggs at 10°C to 2.45 for 341-mg eggs at 12.5°C (Table 1). Analysis of variance indicated that values for K_D at MAWW increased significantly both with temperature ($p < 0.01$) and with initial egg weight ($p < 0.05$).

The ratio of tissue to total alevin weight increased with time and temperature but decreased with initial egg weight. The equation

$$(6) \quad P_T = -449 + 95.4 \ln d + 11.9T - 0.0565W$$

explained 95.6% of the variability in the data ($n = 154$). Mean P_T at MAWW can be predicted from the pooled data by substituting equation (1) for ln d in equation (6) to yield

$$(7) \quad P_T \text{ at MAWW} = 112 - 2.60T - 0.0076W.$$

Actual values for P_T at MAWW ranged from 72.9% for 384-mg eggs at 12.5°C to 95.6% for 340-mg eggs at 5°C (Table 1). Analysis of variance indicated that P_T at MAWW decreased significantly with temperature ($p < 0.01$) but was not affected by initial egg weight. The semilogarithmic relationship

$$(8) \quad \ln D' = 5.99 - 0.150T \quad (R^2 = 97.5\%;\ n = 85),$$

where D' is the number of days postfertilization to ponding or peak emergence, provided the best fit to the hatchery data.

Discussion

Initial egg weight has a significant effect on the time it takes chinook alevins to reach maximum wet weight. Alevins from larger eggs require longer to reach MAWW than alevins from smaller eggs. The difference in times to MAWW can be considerable. For example, my results indicate that alevins from 500-mg eggs would take about 31 d longer to reach MAWW at 5°C than alevins from 200-mg eggs (a 16.6% increase in the total incubation period). At 10°C, a difference of about 14 d is predicted. Similar, but much less extensive observations, have been reported for two other salmonid species. Smith (1958) noted that rainbow trout alevins hatched from large eggs required longer to reach maximum dry weight than alevins from small eggs. Bagenal (1969) indicated that alevins of brown trout (*Salmo trutta*) from large eggs survived longer without food than alevins from small eggs. It is not surprising that the duration of yolk absorption is longer for alevins from larger eggs than for alevins from small eggs, since there is more yolk to be absorbed. The largest chinook eggs used in the current study initially contained more than three times as much yolk as the smallest. What is interesting is that the differences in times to MAWW for the various egg sizes were as small as they were. Yolk is obviously utilized at a more rapid rate by alevins from large eggs than by alevins from small eggs. Exactly how this occurs is not clear but probably is related to the greater surface area of the yolk, over which absorption can occur, in larger eggs.

The voluntary emergence of chinook alevins from gravel is closely correlated with the attainment of maximum wet weight (Heming 1982). Similarly, the optimum time to initiate feeding under laboratory conditions appears to be about the time MAWW is reached. Heming et al. (1982) reported that presenting food prior to MAWW had little or no effect on chinook growth or survival but that delaying food presentation until after MAWW significantly reduced subsequent biomass. Heming et al. (1982) proposed, on the basis of these results, that hatchery production could be maximized if food was presented initially at times described by the equation

$$(9) \quad F = 1201 - 20.3T$$

where F is the time of first feeding in accumulated thermal units (°C·d) and T is the mean incubation temperature. However, the ponding times predicted by equation (9) do not agree well with current hatchery practices (see introduction).

The results of the current study suggest that this discrepancy can be attributed to differences in initial egg weight. Heming et al. (1982) used very large eggs (mean initial wet weight of 490 mg) in their experiments. My results predict that alevins from such large eggs should take a relatively long time to reach MAWW. Indeed, if Heming's (1982) times to MAWW are adjusted for initial egg size, they are not significantly different from those I observed. The actual mean ponding times for chinook in British Columbia hatcheries are, in turn, within the range of times to MAWW predicted for alevins from eggs with initial weights between 200 and 500 mg (Fig. 3). Hatchery managers tend to pond alevins near the lower limit of the range of the predicted times to MAWW, probably because the decision to pond is based on the appearance of the most advanced alevins in a group: likely those hatched from the smallest eggs.

Heming et al. (1982) proposed that the developmental index (K_D) and the ratio of tissue wet weight to total wet weight (P_T) could serve as useful indicators of when chinook alevins should be ponded. They recommended that alevins be ponded at a K_D between 2.2 and 2.3 and a P_T between 79 and 84%. However, in chinook, P_T at MAWW is significantly affected by temperature,

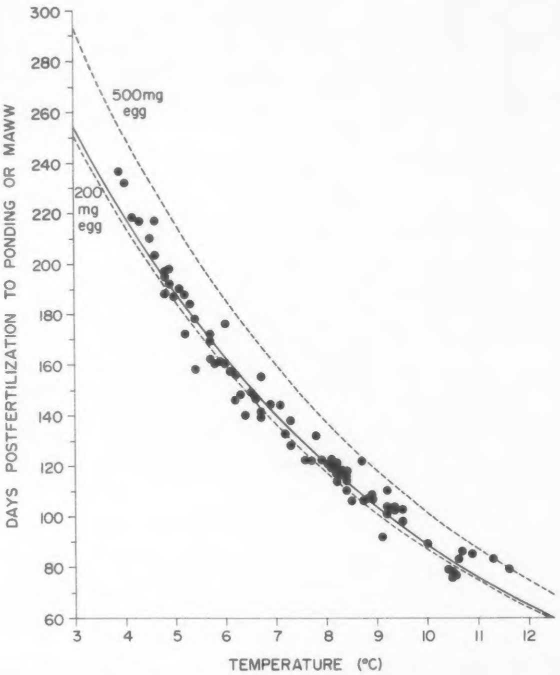

FIG. 3. Relationship between temperature and actual ponding times for chinook alevins at various hatcheries throughout British Columbia. The solid line is the fitted curve, ln $D' = 5.99 - 0.150T$, for the actual hatchery data. The broken lines are the predicted curves of time to MAWW for alevins from 200-mg eggs and 500-mg eggs.

while K_D at MAWW varies significantly with both temperature and egg size. Values for K_D at MAWW ranged between 2.06 and 2.45 and values for P_T ranged between 72.9 and 95.6% in the current study. The ranges are so large that neither indicator is particularly useful unless temperature and initial egg size are taken into account. Bams (1970) proposed that K_D could be used as a general indicator of fry quality in salmonids. My results indicate that unless conditions are carefully controlled, K_D values are of questionable utility.

The relationship I observed between time to MAWW, temperature, and initial egg size can be used to predict optimum ponding times for chinook salmon. Ponding times can be predicted directly from equation (1) if eggs are of relatively uniform size and their mean initial weight is known. Results from production trials at Nitinat Hatchery, Vancouver Island, B.C., suggest that sorting eggs into size groups and ponding each group at MAWW may be a practical means of optimizing production when there are large differences in egg size (K. Peterson, Manager, Nitinat Hatchery, pers. comm.). However, eggs are not segregated according to size at most hatcheries. As a result, there may be up to a month's difference between when alevins from the largest and smallest eggs of the same egg-take reach MAWW. If alevins are ponded according to equation (1) using the mean initial egg weight, then 50% of the individuals will have passed MAWW and potential biomass will be reduced. Biomass can be optimized by ponding when the smallest alevins in the group reach MAWW. Heming et al. (1982) showed that while initiating feeding prior to MAWW did not enhance growth, it did not have any detrimental effects. In practice, optimum ponding times for alevins from eggs of varying sizes can be predicted by using the lower 95% confidence limit for egg size in equation (1). In instances where initial weights are not known, optimum ponding times can be estimated by assuming an initial weight of 200 mg for the smallest eggs. Equation (1) then abbreviates to

$$(10)\quad \ln D = 5.98 - 0.152T.$$

An initial egg weight of 200 mg was selected because it is close to the lower size limit for chinook eggs in southwestern British Columbia. The validity of this choice is supported by the fact that ponding times predicted using equation (10) are not significantly different from the ponding times found by experienced managers to maximize production (equation (8); Fig. 3).

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Survival of Eggs and Alevins of Atlantic Salmon (*Salmo salar*) in Relation to the Chemistry of Interstitial Water in Redds in some Acidic Streams of Atlantic Canada

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Eggs of Atlantic salmon (*Salmo salar*) were incubated in spawning areas of five streams of mean pH 4.6–6.5. Hatching success (36.6–88.7%) for eggs planted after fertilization in the natural substrate of four acidic streams was highly correlated with the pH (4.5–5.0) of interstitial water, and the LL50 was about pH 4.7. Dissolved oxygen concentrations ($>6.0\ \text{mg}\cdot\text{L}^{-1}$) in the interstitial water in these streams were probably not limiting to embryos before hatching. In a near-neutral stream (pH 6.5), the comparatively lower hatching success (5.6–77.0%) was significantly correlated with minimum dissolved oxygen concentration ($1.4–9.2\ \text{mg}\cdot\text{L}^{-1}$) in the interstitial water, and the mean survival of embryos was very low (16.2%) at oxygen concentrations $<6.0\ \text{mg}\cdot\text{L}^{-1}$. Conditions in the substrate where eggs were incubated until hatching were representative of those in natural salmon redds. In one of the acidic streams (pH 4.8), dissolved oxygen concentrations in the interstitial water were low ($2.0–7.6\ \text{mg}\cdot\text{L}^{-1}$) after the hatch, and the emergence of salmon fry from natural redds was minimal, which indicated a low survival of alevins. Estimates of critical pH levels for salmon embryos differ between the laboratory and field approach and are probably site specific because survival in acid waters is determined by acidity, related chemical factors, and changes in water quality within the redd environment.

Des œufs de saumon de l'Atlantique (*Salmo salar*) ont été incubés dans des frayères de cinq cours d'eau à pH moyen de 4,6–6,5. Le succès d'éclosion (36,6–88,7 %) des œufs placés après fécondation dans le substrat naturel de quatre cours d'eau acides présentait une forte corrélation avec le pH (4,5–5,0) des eaux interstitielles ; le NL50 se situait à pH 4,7 environ. La teneur en oxygène dissous ($>6,0\ \text{mg}\cdot\text{L}^{-1}$) des eaux interstitielles ne constituait probablement pas un facteur limitatif pour les embryons avant éclosion. Le succès d'éclosion comparativement faible (5,6–77,0 %) dans un autre cours d'eau à pH presque neutre (6,5) présentait une corrélation significative avec la teneur minimum en oxygène dissous ($1,4–9,2\ \text{mg}\cdot\text{L}^{-1}$) des eaux interstitielles et la survie moyenne des embryons était très faible (16,2 %) aux teneurs en oxygène inférieures à $6,0\ \text{mg}\cdot\text{L}^{-1}$. Les conditions du substrat où les œufs ont été incubés jusqu'à éclosion étaient représentatives de celles des lits des frayères naturelles du saumon. La teneur en oxygène dissous des eaux interstitielles de l'un des cours d'eau acides (pH 4,8) était faible ($2,0–7,6\ \text{mg}\cdot\text{L}^{-1}$) après l'éclosion et l'émergence des alevins des lits de frayères naturelles était très faible, ce qui indiquait un faible taux de survie des jeunes alevins. Les pH critiques pour les embryons de saumon diffèrent selon qu'ils ont été estimés en laboratoire ou sur la terrain. Ces pH sont probablement spécifiques au lieu car la survie en eaux acides est déterminée par l'acidité des eaux, des facteurs chimiques connexes et des modifications de la qualité de l'eau dans l'environnement du lit de la frayère.

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Rivers on the Atlantic side of mainland Nova Scotia underlain by Devonian granite and metamorphic rocks have shown a significant degree of acidification in the past three decades (Farmer et al. 1980; Thompson et al. 1980; Kerekes et al. 1982; Watt et al. 1983). The annual mean pH of precipitation in Nova Scotia is in the range of 4.4–4.6, resulting in high atmospheric acid loading (CANSAP 1980). The input of weak acids from peat deposits and bogs common in this area of Nova Scotia may also contribute to the pH of these organic (colored) waters that have extremely low calcium concentrations. Thirty-seven rivers known for Atlantic salmon (*Salmo salar*) angling flow through this region of Nova Scotia, and in those rivers of pH ≤ 5.0, the salmon resources have either disappeared or declined (Farmer et al. 1980; Watt et al. 1983).

Atlantic salmon are known to be sensitive to acidification and low pH, but levels of acidity lethal to the various freshwater stages have generally been <pH 4.5 in single-factor laboratory studies (Daye and Garside 1977, 1979, 1980; Johansson et al. 1977; Carrick 1979; Daye 1980, 1982; Peterson et al. 1980; Saunders et al. 1983). However, comparisons of the laboratory-derived relationships with the little field data that exist (Hagen and Langeland 1973; Leivestad and Muniz 1976; Leivestad et al. 1976; Grande et al. 1978; Farmer et al. 1980; Harriman and Morrison 1982; Watt et al. 1983) indicate that low lethal pH

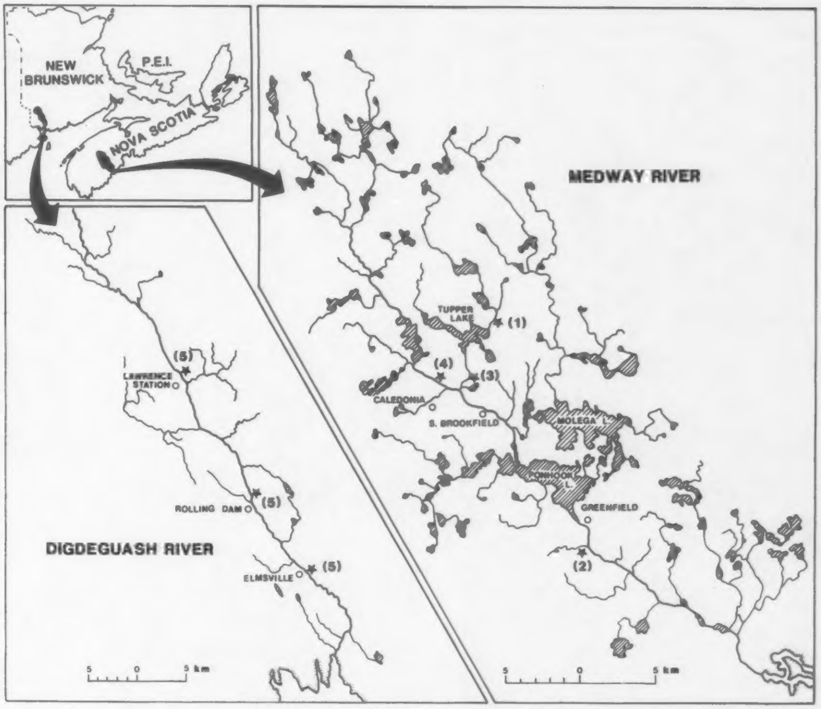

FIG. 1. Study streams (1–5) and egg planting sites (★). 1, Halfway Brook; 2, Fifteen Mile Brook; 3, Westfield River; 4, Medway River; 5, Didgeguash River.

levels for Atlantic salmon are often higher in situ than in the laboratory bioassays. This discrepancy is apparently larger during the embryonic stages than the free-swimming stages. Salmon eggs buried in the gravel beds of streams are vulnerable, particularly to seasonal or episodic changes in the quality of the water (Peterson et al. 1982). The chemistry of interstitial water in spawning substrate may reflect ambient pH fluctuations in streams and localized changes within the redd environment during egg incubation. Therefore, I examined the effects of acidity, in combination with other environmental factors, on survival of Atlantic salmon eggs and alevins within the gravel of the redd.

Materials and Methods

Atlantic salmon eggs were buried in lots of 400 eggs at a depth of 20–25 cm in the gravel of five streams of differing pH. Ten lots of eggs were planted in excavations approximating natural redds in each of four streams of the Medway River system in Nova Scotia, and 20 lots were planted in the Digdeguash River in New Brunswick during November 1980 (Fig. 1). Salmon eggs of Digdeguash River parentage were obtained from the North American Salmon Research Centre, N.B., and planted on 4–5 November at a water temperature of 5°C in three sites in the Digdeguash River (stream 5). Eggs of Medway River parentage were obtained from the Coldbrook Fish Culture Station, N.S., and planted in Halfway Brook (stream 1) and in the Westfield River (stream 3) at 6°C on 8 November and in Fifteen Mile Brook (stream 2) and in the Medway River (stream 4) at 4 and 6°C, respectively, on 11 November. Eggs of either stock were obtained by stripping and "dry" fertilization, water-hardened at the hatcheries (2 h), and transported in water of near-neutral pH maintained at 5–7°C. Planting sites were selected subjectively as suitable spawning areas for salmon. The eggs were buried loosely in the gravel beds using a stovepipe of 45-cm diameter and the method described by Peterson (1978). Areas of streams 2, 3, 4, and 5 used for planting eggs were also used by salmon for spawning but there was no evidence of salmon spawning in stream 1, the most acidic of the study streams. The substratum of these streams was composed mostly of granite, quartzite, slate, and schist.

Water samples for chemical analyses of stream water (pH, alkalinity, conductivity, apparent color, and major ion analyses) were collected at mid-depth in the main channel from each of the five streams, periodically until the eggs hatched ($N = 5–8$). Samples for heavy metal analyses were collected in acid-washed 500-mL polyethylene bottles and preserved with 1 mL of concentrated Aristar® nitric acid. All bottles were rinsed at least thrice with stream water before final filling. Chemical analyses were performed by Environment Canada, Inland Waters Directorate, Water Quality Branch, Moncton, N.B., according to the IWD *Analytical Methods Manual* (Anonymous 1979). The total acid extractable concentrations of heavy metals were determined by atomic absorption spectroscopy. Stream pH (Orion model 399A pH meter with Ingold series 512 low conductivity combination glass electrode), temperature and dissolved oxygen (YSI model 57 oxygen meter), and conductivity (YSI model 32 conductance meter) were measured in situ during each sampling event. During most

TABLE 1. Quantitative chemical analyses (mean ± SD) in the five study streams, November 1980 – May 1981 (units are mg·L^{-1} unless otherwise indicated).

	Halfway (1)	Fifteen Mile (2)	Westfield (3)	Medway (4)	Digdeguash (5)
Stream order	2	2	3	3	3
pH	4.58±0.10[a]	4.73±0.14	4.78±0.17	5.00±0.22	6.47±0.25[b]
Ca	0.67±0.09	0.64±0.07	0.71±0.08	0.85±0.09	3.6±0.16
Mg	0.43±0.07	0.43±0.06	0.48±0.07	0.52±0.08	0.71±0.08
Na	2.5±0.23	3.1±0.33	2.5±0.20	2.8±0.19	1.9±0.19
K	0.3±0.07	0.1±0.04	0.3±0.08	0.3±0.04	0.2±0
SO_4	4.4±0.47	3.7±0.34	4.1±0.36	3.9±0.47	3.8±0.25
Cl	3.2±0.30	4.4±0.62	3.2±0.30	4.1±0.43	2.7±0.76
Fe	0.15±0.03	0.18±0.05	0.16±0.03	0.16±0.02	0.12±0.05
Mn	0.02±0.01	0.03±0.01	0.02±0	0.04±0	0.02±0.01
Al	0.24±0.05	0.11±0.02	0.21±0.03	0.15±0.02	0.08±0.03
Alkalinity	−1.33±0.34[c]	−0.72±0.26[c]	−0.87±0.37[c]	−0.51±0.30[c]	6.28±1.14[d]
Total hardness	3.44±0.51	3.38±0.36	3.72±0.48	4.24±0.57	11.96±0.80
Specific conductance (μS·cm^{-1})	33.0±5.50	31.8±3.10	30.3±4.40	31.3±3.90	34.5±5.07
Apparent color (rel. units)	60.0±30.8	46.7±20.7	48.3±21.4	46.7±18.6	27.5±9.57
N	5	6	6	6	5

[a] $N = 6$.
[b] $N = 8$.
[c] Gran titration.
[d] Total alkalinity.

sampling events ($N = 5$–6), water samples were taken from a depth of 20–25 cm in the artificial redds. Similar samples were also taken periodically from six natural salmon redds in stream 2 and from nine such redds in stream 3. Interstitial water samples of 50 mL were withdrawn from within the redds with a syringe attached to a 1.5 cm (outside diameter) × 1.0 m closed-chamber standpipe driven into the substratum. Measurements of pH and dissolved oxygen were performed immediately by immersing the respective electrodes directly in the syringe. Temperature was measured using a telethermometer (YSI model 46 TUC) connected to a thermister probe embedded in the tip of the standpipe. Duplicate samples were collected and the pH was subsequently verified at a field laboratory.

Gravel permeability, as developed by Terhune (1958) and described by Peterson (1978), was measured at a depth of 20 cm over each egg deposit in each stream on the last sampling date before the eggs hatched. Permeabilities were standardized to 10°C.

The egg deposits were sampled soon after the eggs hatched: 12–21 April in streams 1, 2, 3, and 4 and 20–22 May in stream 5. Living and dead eggs and alevins were collected using a method similar to that developed by McNeil (1964). A Venturi-type pipe assembly made of PVC plastic and designed under the same principle as McNeil's hydraulic sampler was used in conjunction with a 24.5-kL·h^{-1} portable centrifugal water pump. A circular collecting cage of 60-cm diameter was anchored over the egg deposits which were sampled thrice each.

The proportion of eggs in the recovered fraction that had hatched was used to determine survival and is an estimate of total hatchability (including viability), since hatching had been complete in all egg deposits when sampled. The assumption was made that live and dead eggs and alevins were recovered in the same ratio that they occurred within the egg deposits. Survival may, therefore, be overestimated because of the possible mortality and loss of eggs through predation by macroinvertebrates and other factors causing removal. However, deposits in which the recovered fraction was <50% of the number planted were excluded from analysis. Survival data were analyzed using the arcsine transformation of proportions, except in regressions, to normalize variances.

A survey of conditions in natural Atlantic salmon redds was also conducted in stream 3 during 1981–82. The pH, temperature, and dissolved oxygen content of interstitial water at a depth of 20–25 cm in 34 natural redds were measured on four occasions between spawning and fry emergence. Similar measurements on surface water were made in situ more frequently ($N = 16$) during the same period. Gravel permeability in these redds was measured early in December and in May to assess the physical changes that occurred in redds between spawning and emergence. The emergence of fry from 11 of the natural redds was assessed starting on 12–13 May 1982 using traps and the method described by Peterson (1978), adapted from Porter (1973).

Results

Redd Environment

The four Nova Scotia streams (1–4) varied in pH, with the low order tributary streams being most acidic (Table 1). The ionic composition of these four streams was dominated by Na^+, Cl^-, and SO_4^{2-} whereas Ca^{2+} and SO_4^{2-} were the most important ions in the New Brunswick stream (5). Here the alkalinity was comparatively high and the pH level was above 6.0 at all times. Total Al was high in streams 1–4 and often >200 μg·L^{-1} in the most acidic stream. Iron was slightly elevated in the five streams but was mostly <200 μg·L^{-1}, Mn was moderate (≤40 μg·L^{-1}), and levels of other heavy metals

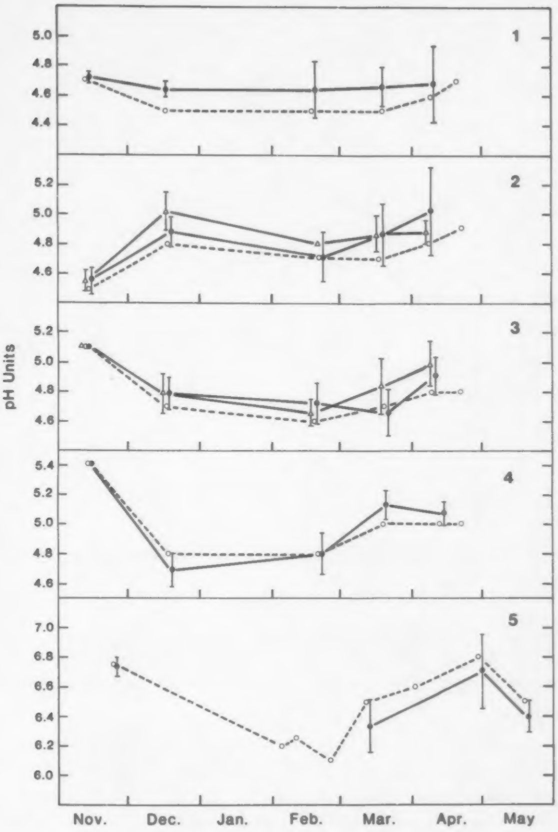

FIG. 2. Temporal variation (1980–81) in pH of study streams 1–5 (○) and of interstitial water in artificial redds (●) and in natural salmon redds (△). Mean ± SD shown for redds. Lines are drawn between points for convenience only.

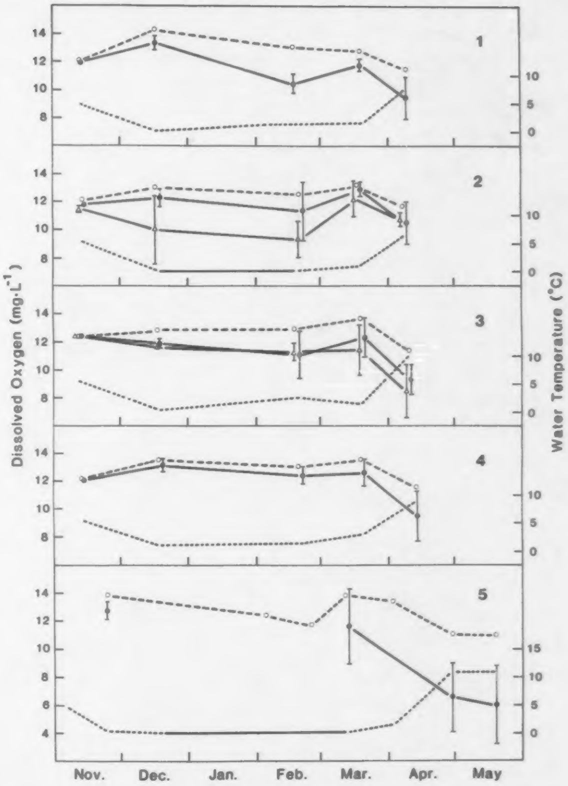

FIG. 3. Temporal variation (1980–81) in dissolved oxygen (○) and temperature (bottom lines) of study streams 1–5 and in dissolved oxygen of interstitial water in artificial redds (●) and in natural salmon redds (△). Mean ± SD shown for redds; solid portion of temperature lines indicates period of ice cover. Lines are drawn between points for convenience only.

were either below detection or very low: Cd $< 1\ \mu g \cdot L^{-1}$, Cu and Pb $\leq 2\ \mu g \cdot L^{-1}$, and Zn $\leq 7\ \mu g \cdot L^{-1}$.

Stream pH fluctuated throughout the period between spawning (egg planting) and hatching (Fig. 2). The pH in stream 2 was lowest during heavy rainfalls in November but increased soon afterward, indicating the rapid response to and flushing of inputs in a small stream. There was a lag in response in the large streams (3 and 4) where the low pH associated with autumn rains was recorded in December. The pH in these streams was also low during February snowmelt. In New Brunswick, pH depressions in stream 5 followed several February thaws and the May freshet. The pH of interstitial water in either natural or artificial redds built of substrate from the streams was generally found to covary with the pH of ambient water in the streams (Fig. 2). However, the mean pH in redds was usually slightly higher than that of surface water in the most acidic streams (1–3). In contrast, the mean pH in redds of stream 5 was less than that of surface water. The mean pH in natural salmon redds generally did not differ significantly from that in artificially made redds (t-test, $P > 0.05$).

Water temperature in the four Nova Scotia streams was generally warmer (overall about 1.5–2.5° higher) than in the New Brunswick stream from November to mid-April (Fig. 3). Therefore, embryos developed more rapidly in streams 1–4 and hatched in April before the water temperature reached 10°C whereas in stream 5, the embryos hatched in May only after the temperature had increased beyond 10°C.

The mean dissolved oxygen concentration of interstitial water in redds of each of the five streams was consistently lower than that of surface water (Fig. 3). Mean oxygen concentrations in natural salmon redds were slightly lower than in the redds where eggs were planted but differences were usually not significant (t-test, $P > 0.05$). Dissolved oxygen concentrations in the streams and in the interstitial water in redds decreased during spring, but remained $> 6.0\ mg \cdot L^{-1}$ in redds of the four Nova Scotia streams as embryos hatched in April. However, the oxygen content of water in redds of stream 5 was markedly less than that of surface water during April–May (Fig. 3), and minimum concentrations were $< 2.0\ mg \cdot L^{-1}$ in some redds by the time embryos hatched.

Gravel permeability was generally high ($> 2000\ cm \cdot h^{-1}$) in most redds, especially in the artificial redds of streams 1–4 (Table 2). Permeability values were lower in natural redds compared with artificial redds in streams 2 and 3, but were lowest in artificial redds of stream 5. This coincides with differences in the dissolved oxygen concentrations of interstitial water between sites.

The more frequent measurements of pH, temperature, and

TABLE 2. Gravel permeability (standardized to 10°C = K_{10}) in natural (N) and artificial (A) redds of the study streams.

Stream	Redd type	$\overline{K_{10}} \pm$ SD ($cm \cdot h^{-1}$)	Sample size	Range
1[a]	A	17054±5866	9	9856 – 26 500
2[a]	N	5156±7827	6	825 – 20 900
	A	11165±7555	10	1705 – 21 450
3[a]	N	4383±4255	9	975 – 14 850
	A	7198+4640	8	2633 – 15 000
4[a]	A	9380±8068	7	1597 – 20 703
5[a]	A	2643±2528	10	556 – 7 750
3	N[b]	5065±5820	33	310 – 22 320
	N[c]	2990±3591	33	153 – 12 520

[a] Sampled in April 1981 before hatch.
[b] Sampled in December 1981 after spawning.
[c] Sampled in May 1982 before emergence.

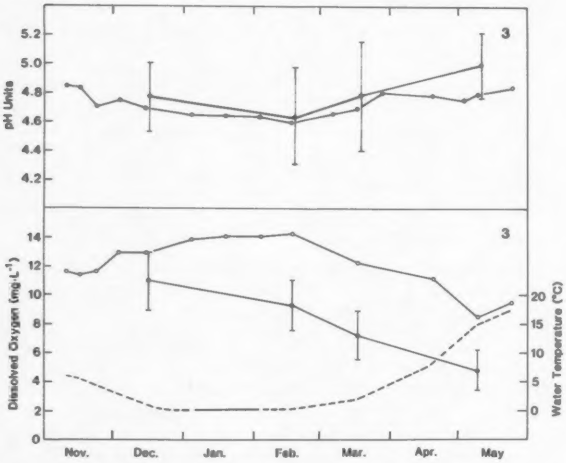

FIG. 4. Temporal variation (1981–82) in pH, dissolved oxygen, and temperature (bottom line) of stream 3 (○), and variation in pH and dissolved oxygen of interstitial water in 34 natural salmon redds (●). Mean ± SD shown for redds; solid portion of temperature line indicates period of ice cover.

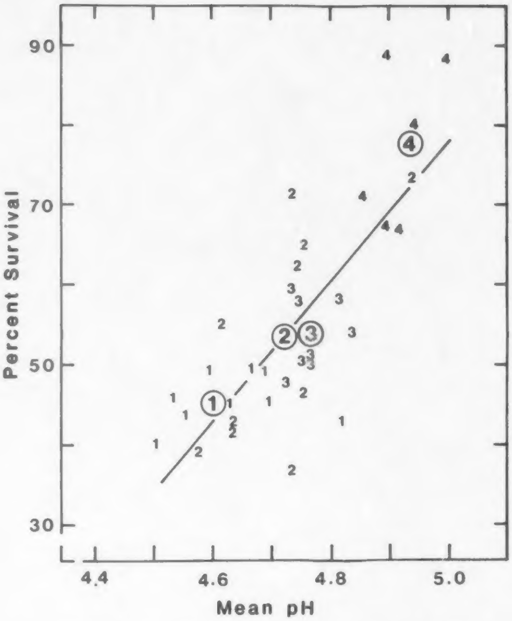

FIG. 5. Hatching success of salmon embryos as a function of mean pH of interstitial water in individual redds of streams 1–4. Bold characters (circled) represent averages for each stream; $y = -356.82 + 86.89x$, $r = 0.78$, $t = 6.95$, $N = 33$.

dissolved oxygen in ambient water in stream 3 during the period between spawning and emergence in 1981–82 (Fig. 4) confirm the trends previously suggested from fewer data points (Fig. 2, 3). Conditions in natural salmon redds of stream 3 were also generally similar to those recorded the previous year in both natural and artificial redds. Additional measurements in redds during May (Fig. 4) indicate that the pH was highest after the hatch, and that the dissolved oxygen concentration decreased further (mean = $4.8 \, mg \cdot L^{-1}$). Gravel permeability in the salmon redds decreased considerably between spawning and fry emergence; permeability values measured before emergence were also lower than those recorded the previous year, before hatching, in both natural and artificial redds of stream 3 (Table 2).

Hatching Success and Emergence

The hatching success of embryos incubated from fertilization in redds of natural substrate in the four Nova Scotia streams (1–4) ranged from 36.6 to 88.7% and was highly correlated with mean pH in redds (Fig. 5; $r = 0.78$, $P < 0.001$). Data for redds in streams 1–4 were combined to calculate the regression. The mean survival was 77.8% at mean pH 4.92 in redds of stream 4, 53.5 and 53.3% at pH 4.77 and 4.72 in streams 3 and 2, respectively, and 45.5% at pH 4.64 in stream 1. The minimum dissolved oxygen concentration in redds was $>6.0 \, mg \cdot L^{-1}$ and did not differ significantly (ANOVA, $P > 0.05$) among redds of streams 1–4 (overall mean = 9.86, range = $6.4\text{–}11.2 \, mg \cdot L^{-1}$). There were no significant correlations between survival in redds of streams 1–4 and minimum dissolved oxygen ($r = 0.21$, $P > 0.20$) or gravel permeability ($r = 0.11$, $P > 0.50$).

The survival of embryos in stream 5 (mean = 38.8, range = 5.6–77.0%) was lower than in streams 1–4 at a comparatively high pH in redds (mean = 6.52, range = 6.32–6.69). Survival was not correlated with mean pH in redds ($r = 0.29$, $P > 0.20$) but rather was significantly correlated with minimum dissolved oxygen concentration (Fig. 6; $r = 0.71$, $P < 0.01$). The minimum dissolved oxygen was significantly lower in redds of stream 5 than of streams 1–4 (ANOVA and Newman–Keuls test, $P < 0.05$), and lowest concentrations (mean = 6.2, range = $1.4\text{–}9.2 \, mg \cdot L^{-1}$) occurred in April– May, before the eggs hatched. Gravel permeability was also lowest in redds of stream 5, often $<2000 \, cm \cdot h^{-1}$ (Table 2). The mean survival in redds of stream 5 with minimum dissolved oxygen concentrations < $6.0 \, mg \cdot L^{-1}$ was only 16.2% ($N = 5$).

The first emergent fry from natural salmon redds of the 1981 autumn spawning in stream 3 were captured on 14 May 1982 (~185 d from median spawning date), and emergence continued until 25 May. The number of fry captured ranged from 0 to 161 per redd, but emergence values are underestimates, since the traps were not completely successful in retaining all fry as

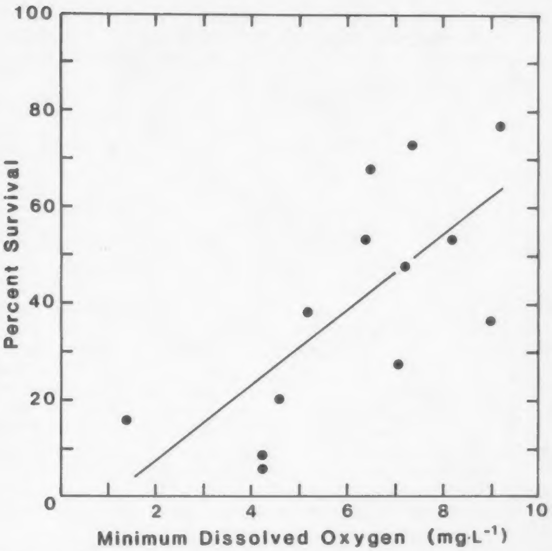

FIG. 6. Hatching success of salmon embryos as a function of minimum dissolved oxygen of interstitial water in individual redds of stream 5; $y = -8.02 + 7.79x$, $r = 0.71$, $t = 3.38$, $N = 13$.

the water level dropped late in May. Fry emerged from 8 of the 11 sampled redds, and redds from which no emergence occurred had very low gravel permeability ($<500\,\mathrm{cm \cdot h^{-1}}$) at the expected time of emergence. The mean pH of interstitial water was about 4.8 during incubation, and dissolved oxygen concentrations in redds were low (range = $2.0\text{–}7.6\,\mathrm{mg \cdot L^{-1}}$) before emergence.

Discussion

The hatching success of Atlantic salmon embryos, incubated in the natural substrate of acidic streams, was directly related to the mean pH of interstitial water percolating through the substratum. The LL50 was approximately pH 4.7 whereas, at pH 5.0, survival was >75%. The sensitivity of Atlantic salmon embryos to pH stress alone is known to be dependent on the stage of development, with low lethal limits varying between pH 3.0 and 3.6 in short-term exposures and increasing to higher levels for continuous exposure from fertilization to hatching (Daye and Garside 1977, 1979; Carrick 1979). The LL50 value of low pH for hatching of Atlantic salmon embryos subjected to continuous exposure from fertilization was 3.9 in one study (Daye and Garside 1979) and always <4.5 in other bioassays, with no obvious difference in hatching attributable to acidity at pH ≥ 4.5 (Carrick 1979). The LL50 value for H^+ toxicity can thus be up to six times more acidic in laboratory bioassays than the present assessment in acidic streams. The effect of acidity on salmonid embryos can be mitigated by calcium but the concentration must be at least $>1\,\mathrm{mg \cdot L^{-1}}$ to have a moderating effect on H^+ toxicity (Brown and Lynam 1981). The beneficial effects of calcium on embryo survival were probably minimal in the soft waters of streams 1–4 ($Ca^{2+} < 1.0\,\mathrm{mg \cdot L^{-1}}$). The higher LL50 of pH may then be a result of low ionic content of acidic water in these streams (conductivities ~ 30 μS) compared with the acidified tap water used in some laboratory tests, e.g. conductivities of 60–124 μS reported by Daye and Garside (1979). This is further supported by Carrick's (1979) report of a substantial increase in salmon egg mortality at pH 4.0 by dilution of assay water to half ionic strength. Conversely, an increase of dissolved salts in soft water has been shown to improve the survival of salmonid eggs at low pH (Bua and Snekvik 1972).

In natural environments, salmon embryos may be subjected to changes in other variables in addition to pH. Changes in the quality of the stream water such as the pH-related mobilization of aluminum may yield some degree of aqueous aluminum toxicity or synergism with low pH, but apparently not until after the embryos have hatched (Baker 1982). A twofold difference in aluminum concentration at similar pH levels in streams 2 and 3 (Table 1) did not result in additional mortality, possibly because of its positive effect on embryo survival at pH levels <5.0 (Baker and Schofield 1980, 1982). The high levels of dissolved organic material in streams 1–4 (usually $>10\,\mathrm{mg\ C \cdot L^{-1}}$; G. L. Lacroix, unpubl. data) also suggest that a fair proportion of the aluminum is chelated to the organics and are hence nontoxic (Baker and Schofield 1980; Driscoll et al. 1980; Van Coillie et al. 1983). Concentrations of other heavy metals in the streams were below those considered as toxic to salmonid embryos (Alabaster and Lloyd 1980; Spry et al. 1981) but the precise toxicity of iron is not known.

Localized changes in the redd environment may also alter some factors and their effects on eggs. Studies of the hyporheal zone in streams of various types have shown that both pH and oxygen decline with depth, and that carbon dioxide rises (reviewed in Williams and Hynes 1974; Hynes 1983). Similar changes may also occur in interstitial water in redds of salmonids because of respiratory exchanges, aerobic bacterial decomposition, and to a limited extent, abiological oxidation of dissolved organic materials. Oxygen in interstitial water in redds was always less than that in ambient water in each of the streams, lowest in redds with low gravel permeability and at high temperature. Such processes may also partly explain why the pH of interstitial water in redds was usually lower than that of ambient water in the near-neutral stream but more often higher in redds than in the water above in the acidic streams. Aerobic decomposition of organic matter in interstitial water can decrease alkalinity and pH in water of pH >5.0 whereas, in water of pH 4.5–5.0, it leads to either minimal change in pH or an increase in alkalinity and pH from the uptake of H^+ if respiration releases NH_4^+ (Stumm and Morgan 1981). The substrate may also have slight buffering effects in the acidic streams dependent on the rate of renewal of water in the redds.

As a result of high gravel permeability in these Nova Scotia streams, the oxygen in redds did not reach the limiting levels for prehatching eggs (Davis 1975). It follows that carbon dioxide levels in redds, also because of adequate water exchange from stream to substratum, were below those that would inhibit oxygen uptake of salmonid eggs and increase mortality of embryos (Alderdice and Wickett 1958). Hence, the lethal effects on embryos in streams 1–4 were mainly from H^+ toxicity. The high threshold for pH effects was thus probably a function mostly of the low calcium concentration in these streams.

The low overall survival (38.8%) of salmon eggs in the near-neutral stream in New Brunswick apparently resulted from a decrease of dissolved oxygen in some redds to concentrations lower than the incipient limiting level of $5.93 \pm 1.01\,\mathrm{mg \cdot L^{-1}}$ for mature (prehatching) salmonid eggs (Davis 1975). The mean embryo survival in redds with dissolved oxygen concentrations below this limiting level was only 16.2%, and the estimated concentration for 50% survival was $7.4\,mg\cdot L^{-1}$. Other experiments also indicate that survival of salmonid embryos in gravel beds is related to oxygen content in interstitial water, and mean concentrations necessary for high survival (>50%) may exceed $8.0\,mg\cdot L^{-1}$ (Coble 1961; Phillips and Campbell 1962). Low dissolved oxygen concentrations in interstitial water could therefore have a considerable effect on embryo survival in addition to the effect of H^+ in some acidic streams, especially those with low gravel permeability. However, a temperature regime that favors a more rapid development, e.g. 35–40 d less for hatching in the Nova Scotia streams than in the New Brunswick stream, decreases the probability of exposure of eggs to adverse levels of oxygen, and possibly of carbon dioxide, common in substratum during spring.

Emergence of Atlantic salmon fry from natural redds was observed in stream 3, but even though they are underestimates, the numbers of emergent fry were very low. There was no emergence from redds with extremely low gravel permeability ($<500\,cm\cdot h^{-1}$). Similarly, Peterson (1978) obtained no fry emergence from salmon eggs planted in gravel of a nonacid river with a mean permeability of $600\,cm\cdot h^{-1}$. Conditions in natural redds of stream 3, however, indicate that considerable mortality of alevins may also have resulted from the combined effects of the low pH (overall mean near 4.8) and other factors. Dissolved oxygen in the interstitial water decreased after the hatch (mean $4.8\,mg\cdot L^{-1}$ in May), and carbon dioxide probably increased. The effects of these factors are also enhanced by an increased sensitivity of newly hatched alevins over that of embryos to low oxygen (Davis 1975) and to low pH (Leivestad et al. 1976; Daye and Garside 1977, 1979; Peterson et al. 1982), and by a lack of resistance adaption of alevins to low pH (Daye 1980). There was also some possibility of aluminum toxicity to alevins. In contrast with embryos, alevins are sensitive to aluminum, and concentrations $>200\,\mu g\cdot L^{-1}$ are usually toxic at low pH levels in soft water, if present as inorganic forms (Baker and Schofield 1980, 1982; Brown 1983). Although much of the total aluminum measured in the stream was possibly organically complexed, the potentially toxic fractions of aluminum are, at times, more elevated in the interstitial water of spawning substrate than in ambient water (Gunn and Keller 1984).

Conditions in artificial redds used to access the effects of the environment on salmon eggs were generally representative of those in natural redds, although conditions in artificial redds exhibited slightly less variability, and survival values in the present study should be applicable to natural populations in these rivers. The interaction between acidity and related chemical factors and the changes in water quality possible within the redd environment may explain the variability in estimates of critical pH values for salmonid embryos and suggest that no simple acid threshold can be set for their survival in different locations.

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Cellular Phosphorus Concentration as a Criterion for Trophic Status in Rapidly Flushed Lakes

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Uttormark, P. D., and M. L. Hutchins. 1985. Cellular phosphorus concentration as a criterion for trophic status in rapidly flushed lakes. Can. J. Fish. Aquat. Sci. 42: 300–306.

By using the steady-state concentration of cellular phosphorus(P) as the indicator of a lake's trophic status, we derived equations that describe the flushing rate at which cellular washout might be expected, and the range of flushing rates in which cellular P concentrations would be reduced significantly below those of total P. Calculated concentrations of cellular P and total P are virtually identical for lakes with flushing rates below about 10 yr^{-1}; at higher rates they may differ substantially. The P mass balances equations we developed consider total P to consist of two components: cellular P and available P. Lakes are treated as completely mixed flow-through reactors with constant P influx. The equations describe conditions in which available P remains in solution until it is removed by algal uptake or lost through sedimentation or outflow. Algae are lost from the system by sedimentation or are discharged through the lake outlet. The transfer of P from available to cellular forms is described by Michaelis–Menten growth kinetics.

Nous avons utilisé la concentration à l'équilibre du phosphore cellulaire (P) comme indicateur de l'état trophique d'un lac pour obtenir des équations décrivant le taux de renouvellement auquel on peut prévoir un « lessivage » cellulaire ainsi que la gamme des taux de renouvellement où la concentration cellulaire de P serait réduite de façon appréciable en deçà de celle du P total. Les concentrations calculées de P cellulaire et de P total sont pratiquement identiques dans les lacs à taux de renouvellement inférieur à environ 10 ans^{-1} ; elles peuvent différer de façon appréciable aux taux supérieurs à cette valeur. Dans les équations d'équilibre massique du P que nous avons élaborées, le P total a deux composantes : le P cellulaire et le P disponible. Les lacs sont considérés comme des réacteurs sans recirculation à contenu homogène et à apports constants de P. Les équations décrivent les conditions dans lesquelles le P disponible demeure en solution jusqu'à son absorption par les algues on sa perte par sédimentation ou sortie du lac. Les algues quittent le système par sédimentation ou rejet avec les eaux de sortie du lac. Le passage du P de la forme disponible à la forme cellulaire est décrit par la cinétique de croissance de Michaelis–Menten.

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Empirically determined estimates of a lake's steady-state total phosphorus(P) concentration provide a reasonable index of its trophic condition, as shown by Vollenweider (1975, 1976), Dillon and Rigler (1974), and others. These investigators developed mass balance equations for calculating steady-state P concentrations and demonstrated that the results applied reasonably well to lakes having a broad range of flushing rates and P loadings. The equations they developed have also been used by lake managers to estimate the degree of P abatement necessary to achieve various levels of water quality improvement. Of particular interest has been the improvement of lakes through the reduction of algal populations. The equations have proven to be useful tools for these types of management deliberations because of the apparent correlation between calculated steady-state P values and the observed "severity of problems" due to excessive algal growth in lakes. However, as noted by Vollenweider (1976), there is a set of lakes for which this relationship potentially breaks down: lakes with high flushing rates. For these lakes, cellular losses through the outlet reduce algal populations to levels below that which could theoretically be supported by the amount of P present. In extreme cases, when cellular loss exceeds growth, complete "washout" of algae is possible regardless of P concentrations.

Our objective was to quantify "high flushing rates." In particular, we aimed to describe conditions under which (1) cellular washout might be expected and (2) cellular concentrations might be depressed below levels suggested by the steady-state P concentration.

Theoretical Development

Vollenweider (1975, 1976), Dillon and Rigler (1974), and others described the mass balance of total P in a lake as

$$(1) \qquad \frac{dP_t}{dt} = \rho P_0 - \sigma P_t - \rho P_t$$

where P_t = total phosphorus concentration in the lake, P_0 = phosphorus concentration in the inflow, and σ and ρ are rate coefficients for sedimentation and flushing, respectively.

In developing Eq. 1 it was assumed that on a long-term basis, lakes could be approximated by completely mixed flow-through reactors. It was further assumed that the influx of P was constant and that P losses occurred through the outlet and through internal sedimentation at rates directly proportional to the amount of P in the lake. Under these assumptions, the steady-state P concentration was selected as an indicator of trophic status. At steady-state,

$$(2) \quad P_t = P_0 \frac{\rho}{\sigma + \rho}.$$

Thus, the in-lake concentration is always less than the concentration in the inflowing water by an amount which depends on the magnitude of the sedimentation rate coefficient, σ, and the flushing rate, ρ.

The alternative theoretical development we propose is similar to that described. The principal difference is that total P is divided into two parts, cellular P and free available P, and mass balance equations are written which account for each of these components. We recognize that this classification does not correspond exactly to the chemical subdivisions of P commonly reported for lakes; nevertheless, we chose to use those terms because they described precisely what we mean in the mathematical analysis, and at the same time, they alert the reader of the necessity to temper interpretation of theoretical results with practical understanding of lakes.

For purposes of this analysis, we represented total P by the sum of two components:

$$(3) \quad P_t = P_x + P_s$$

where P_x represents P contained within algal cells and P_s represents dissolved P which is available for algal growth. Also,

$$(4) \quad P_x = \frac{X}{Y}$$

where X denotes the concentration of algal cells and Y is the yield coefficient for P which we treated as a constant.

We also assumed that P_0, the concentration of total P in the inflowing waters, is made up of available P and viable algal cells such that

$$(5a) \quad P_0 = P_{s0} + P_{x0}$$

where the subscript "0" refers to the inflow. For convenience, we let

$$(5b) \quad P_0 = aP_0 + bP_0$$

where $a + b = 1$ and where a and b denote the distribution of P between available and cellular forms, respectively. We then formulated a pair of mass balance equations, one for substrate, P_s, and one for cells:

Substrate balance:

Change = inflow − algal uptake − outflow

$$(6) \quad \frac{dP_s}{dt} = \rho P_{s0} - \mu P_x - \rho P_s.$$

Cell balance (expressed as P_x):

Change = inflow + growth − sedimentation − outflow

$$(7) \quad \frac{dP_x}{dt} = \rho P_{x0} + \mu P_x - \sigma P_x - \rho P_x.$$

In both these equations, μ is the specific growth rate for algae as defined by the Michaelis–Menten relationship

$$\mu = \frac{\hat{\mu} P_s}{K_s + P_s}$$

where $\hat{\mu}$ is the maximum specific growth rate and K_s is the half-saturation constant.

Equations 6 and 7 describe a two-level system composed of P and algae. Phosphorus influx provides the driving force for the system. Phosphorus remains in solution until it is removed by algae or is lost through hydraulic outflow. Phosphorus uptake by algae is defined by Michaelis–Menten kinetics and uptake and growth occur simultaneously. Algae (and the P they contain) are lost through sedimentation and hydraulic outflow.

We then assumed conditions of steady state and combined Eqs. 5, 6, 7, and 8 to yield

$$(9) \quad bP_0^2 + \left[b\left(K_s - \frac{(\sigma + \rho)}{\rho} P_x\right) + \left(\frac{\hat{\mu} - (\sigma + \rho)}{\rho}\right) P_x\right] P_0 - \frac{(\sigma + \rho)}{\rho} P_x \left[K_s + \frac{(\hat{\mu} - (\sigma + \rho))}{\rho} P_x\right] = 0.$$

Equation 9 includes all assumptions and approximations incorporated in the development of Eq. 1, and in addition, the Michaelis–Menten relationship is used to describe the partitioning of P between available and cellular forms. The remainder of this paper deals with solutions to Eq. 9 under differing inflow conditions. Each of these solutions relies on the assumption that the specific sedimentation rate may be approximated by the square root of the flushing rate:

$$(10) \quad \sigma \simeq \sqrt{\rho}.$$

The validity of this assumption is based on the work of Larsen and Mercier (1976) and Vollenweider (1976). Those investigators, however, developed their relationships based on the internal loss of total P; by comparison, the equations we developed permit only the internal loss of cellular P. Internal P losses would most likely be associated with cellular P rather than dissolved P for most lakes. Also, this modification reduces the calculated amount of internal P loss for rapidly flushed lakes, thereby making inflow and outflow concentrations of total P more nearly the same. This is consistent with typical field observations.

Equation 9 includes the algal parameters, $\hat{\mu}$ and K_s, in addition to ρ and P_0. Therefore, if our work is to be compared with that of others, we must specify values for the algal growth parameters. Under conditions of continuous light and temperature, many algal species are capable of achieving maximum specific growth rates of $1.0\,d^{-1}$ or even higher. Maximum growth rates under natural conditions would be somewhat lower (Thomann et al. 1975). Considering the natural periodicity of light and temperature, and the long-term nature of the model equations, we selected a value of $\hat{\mu} = 0.25\,d^{-1}$ (i.e. $90\,yr^{-1}$) for use here. Also, it is known that the half-saturation coefficient for P is low, perhaps in the range of $2\text{–}10\,mg \cdot m^{-3}$ (Zison et al. 1978). We used a value of $5\,mg \cdot m^{-3}$. Other values could have been selected, and no special claim is made for the preferability of these values over others. At the same time, we judged these values to be realistic for use in the model equations, and we believe that reasonable comparisons can be made between model results and lake data (see section on sensitivity analysis).

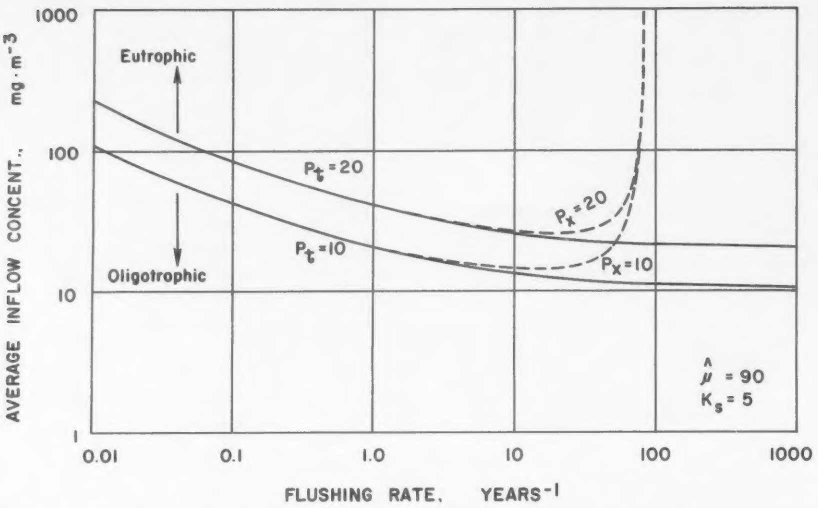

FIG. 1. Calculated steady-state cellular P concentrations (broken lines) as compared with total P concentrations (solid lines) for a lake under the condition that the inflowing waters do not contain algal cells. Values of 10 and 20 $\mathrm{mg \cdot m^{-3}}$ are shown. The two solid lines on the graph are based on Eq. 2 with $\sigma = \sqrt{\rho}$ and are plots of $P_t = 10$ and $20\ \mathrm{mg \cdot m^{-3}}$.

Case 1: No Cells in the Inflow (i.e. $b = 0$)

For the special case where the inflowing waters contain available P but no algal cells, Eq. 9 reduces to

$$(11)\quad P_x = P_0 \frac{\rho}{\sigma + \rho} - \frac{\rho K_s}{(\hat{\mu} - (\sigma + \rho))}.$$

A comparison of Eqs. 2 and 11 shows that cellular P is always less than total P by an amount that depends on ρ, σ, K_s, and $\hat{\mu}$. Also, from Eq. 10,

$$(12)\quad P_x = P_0 \frac{\rho}{\rho + \sqrt{\rho}} - \frac{\rho K_s}{(\hat{\mu} - (\rho + \sqrt{\rho}))}.$$

The use of cellular P, rather than total P, as a criterion for lake condition is illustrated in Fig. 1. The values of 10 and 20 $\mathrm{mg \cdot m^{-3}}$ were introduced by Vollenweider (1975) as "acceptable" and "excessive" with respect to lake eutrophication. The solid lines divide the graph into three zones, and experience has shown that in most instances, data for eutrophic lakes plot above the lines, oligotrophic lakes plot below, and mesotrophic lakes blend in between. The usefulness of these model results as guidelines for lake restoration was reported by Uttormark and Hutchins (1980).

Plots of P_x are virtually identical to those for total P when the flushing rate is less than $10\ \mathrm{yr^{-1}}$; at higher flushing rates, the P_x lines diverge from their P_t counterparts (Fig. 1). This locus of the P_x lines can be explained if one considers the rates of algal growth as compared with the rate of P replenishment in lakes. Algal growth, i.e. the incorporation of available P into algal biomass, is a relatively rapid process which has a time scale in days. In contrast, the rate of P replenishment is related to a lake's flushing rate which may have a time scale as long as tens of years (Lake Superior) or as short as a few days (run-of-the-river impoundments). Only in rapidly flushed lakes are the rates of P uptake and P replenishment similar; P uptake is the much faster process for lakes with low flushing rates. Therefore, for slowly flushed lakes, P uptake by algae is the dominant process and almost all available P would be removed from solution and incorporated in algal biomass. Under these conditions, calculated values of P_x and P_t are virtually identical.

For rapidly flushed lakes, the combined effect of P replenishment and cellular outflow results in conditions whereby only part of the available P is taken up by algae and the rest remains in solution. For the example shown in Fig. 1, this occurs in the range of flushing rates between $10\ \mathrm{yr^{-1}}$ and about $80\ \mathrm{yr^{-1}}$. Since only part of the incoming P is converted to algal biomass, a given level of P influx results in a value of P_x which is less than P_t.

At extremely high flushing rates, greater than $80\ \mathrm{yr^{-1}}$ for the example, cellular losses exceed growth and washout occurs. Under these conditions, the cellular concentration goes to zero and all of the P remains in solution. Washout conditions can be described more completely by solving Eq. 12 for the flushing rate which causes P_x to vanish. Using ρ_w to denote the minimum flushing rate at which washout occurs, Eq. 12 may be solved by applying the quadratic formula to yield

$$(13)\quad \rho_w = \left[\frac{-1 \pm \left[1 + \frac{4P_0\hat{\mu}}{(P_0 + K_s)} \right]^{1/2}}{2} \right]^2.$$

Equation 13 describes the maximum flushing rate at which steady-state populations of algae could exist in the system for a given level of P in the inflow and specified algal growth parameters, $\hat{\mu}$ and K_s. Equation 13 suggests that if the flushing rate for a given lake were increased (e.g. by supplementing the inflow) to a level that exceeds ρ_w, algal populations could not sustain themselves despite the presence of P in an available form, and washout would ultimately occur. The total P concentration, however, does not go to zero; it is always described by Eq. 2 regardless of flushing rate. Nevertheless, there is a change in the forms of P which make up the total: cellular P goes to zero and all the P in the system is in the available form when ρ exceeds ρ_w.

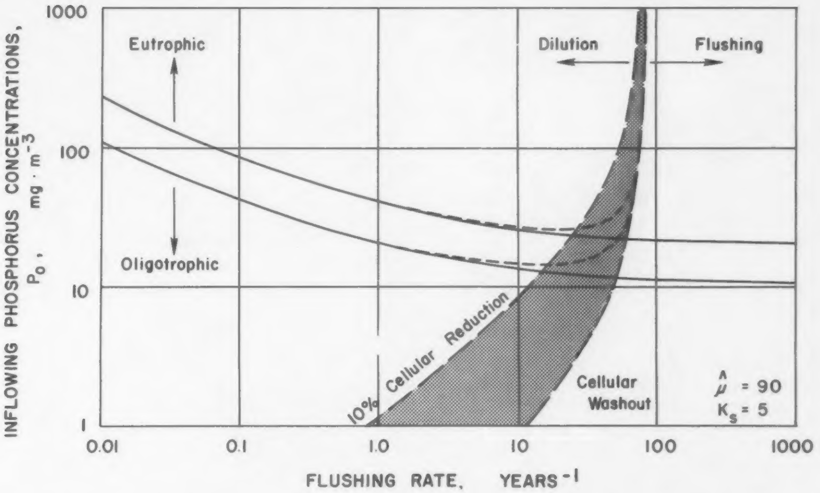

FIG. 2. Cellular washout and cellular reduction (10%) as a function of P influx and flushing rate under the assumption that the inflow is free of cells. This figure contains a shaded area superimposed on Fig. 1. The right-hand boundary of the shaded area depicts cellular washout (Eq. 13). The left-hand boundary is defined by the conditions where the theoretical cellular P concentration deviates from total P by 10% (Eq. 14).

A transition zone in which only part of the incoming P is converted to algal biomass can also be described using Eq. 12. To illustrate this, we arbitrarily defined the boundary of the transition zone to be located where P_x was 90% of P_t. That is, within the transition zone the total P content consists of less than 90% cellular P and more than 10% available P. If ρ_s is used to denote the flushing rate at which P_x departs from P_t by 10%, then by using an approach parallel to that used for cellular washout it can be shown that

$$(14) \quad \rho_s = \left[\frac{-1 \pm \left[1 + \dfrac{0.4 P_0 \hat{\mu}}{(0.1 P_0 + K_s)} \right]^{1/2}}{2} \right]^2 .$$

A more general illustration of the use of cellular P concentration as a criterion for lake condition is shown in Fig. 2. The graph is divided into three zones. To the left of the shaded area, cellular P and total P are virtually identical and available P is negligible. The alternative equations we present in this paper offer no advantage in this zone. Indeed, calculations based on total P would be preferable because the equations are simpler and require fewer input parameters. To the right of the shaded area, cellular concentrations are zero because of washout. In this zone, calculated total P values provide no information regarding cellular concentrations, and the apparent relationship between empirical total P and the severity of algal problems would not apply. The shaded area is a transition zone in which predicted cellular concentrations are not zero, but are lower than the levels supported by the same total P concentrations at lower flushing rates. In this zone, we would expect Eq. 11 to provide a better indicator of trophic condition than Eq. 12; however, corroborating evidence is lacking.

Figure 2 also provides an interesting perspective on dilution/flushing as a lake management technique. This technique involves supplementing a lake's natural inflow with water from a source with a lower nutrient content. The projected benefits are twofold: (1) nutrient concentrations in the lake would be reduced, and thereby support reduced algal populations, and (2) the increased hydraulic flow would cause larger quantities of algae to be discharged through the outlet. The two effects occur simultaneously, however; if the former is expected to dominate, the process is called "dilution." When the latter dominates, it is called "flushing." Attempts are often made to distinguish between the two processes depending on the relative size of the supplemental flow: small flows provide dilution, large flows cause flushing. In Fig. 2, dilution/flushing is treated as a continuum, with dilution on one end of the spectrum and flushing on the other. The necessity of distinguishing between processes is avoided and an intermediate transition zone is defined.

Case 2: Inflow Contains Cells (i.e. $b > 0$)

The model results depicted in Fig. 1 and 2 apply only to situations in which the inflowing waters are free of algae. Although these restrictions would be met in some lake situations, e.g. ponds flushed with municipal drinking water (Green Lake and Wapato Lake, Washington (Welch 1979)), it is far more common for lakes with high natural flushing rates to receive water which contains algae. Many of these lakes are little more than wide spots in rivers.

The importance of cellular inflow on the empirical cellular P concentrations in lakes is illustrated in Fig. 3. For flushing rates less than 10 yr^{-1}, all the plots collapse into a single line. As for case 1, P_x and P_t are virtually identical at low flushing rates. At higher flushing rates, the lines diverge and the paths depend on the concentration of cellular P in the inflow.

When $b = 1.0$, the plots of $P_x = 20$ and $P_t = 20$ are identical for all flushing rates. This result occurs because for $b = 1.0$, the inflow consists totally of cellular P, and the time required for

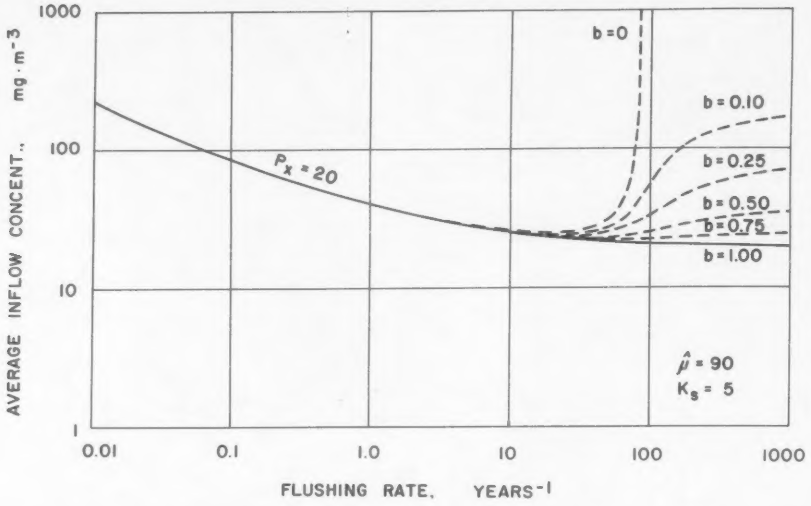

FIG. 3. Combinations of flushing rate and inflowing total P concentration which result in a steady-state cellular P concentration of 20 mg·m^{-3}. Broken lines at the right of the figure are for differing levels of cellular P in the inflow, ranging from 0% ($b = 0$) to 100% ($b = 1.0$). This figure is based on Eq. 9 and contains plots of $P_x = 20$ for situations in which the total P content of the inflowing waters consists of 0, 10, 25, 50, 75, and 100% cellular P.

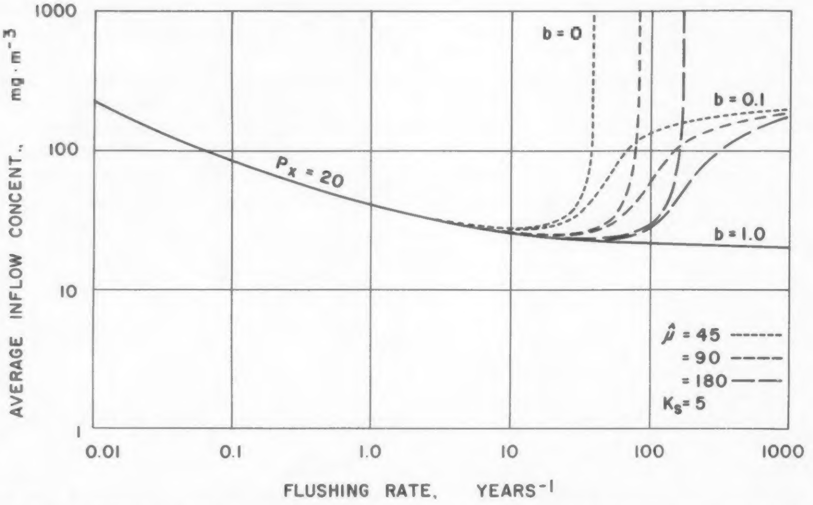

FIG. 4. Sensitivity analyses showing the effect of the maximum specific growth rate on calculated values of in-lake cellular P when 0, 10, and 100% of the inflowing P is in the cellular form.

algal growth to occur, the reason P_x departs from P_t at high flushing rates, is irrelevant.

At extremely high flushing rates, all curves approach a value of P_0 equal to P_x/b. For example, for $b = 0.1$ the plot of $P_x = 20$ approaches $P_0 = 200$. Or put another way, if 10% of the total P influx is in a cellular form, then a total P concentration of 200 mg·m^{-3} is needed to maintain a cellular P concentration of 20 mg·m^{-3} in the lake. This result occurs because the residence time for algae in the lake is too short to permit growth despite the abundance of available P in solution. Of course, cellular washout is not possible even at extreme flushing rates when the inflow contains cells, because cells lost through outflow and sedimentation are replenished continually by the inflow.

In summary, from the analysis we suggest that at high flushing rates, the concentration of cellular P in a lake would be less than that of total P by an amount which depends on the concentration of cellular P in the inflow as well as the algal growth rates. At low flushing rates, calculated levels of cellular P and total P are identical, and while these levels are dependent on the concentration of total P in the inflow, they are independent of its distribution between cellular and available constituents.

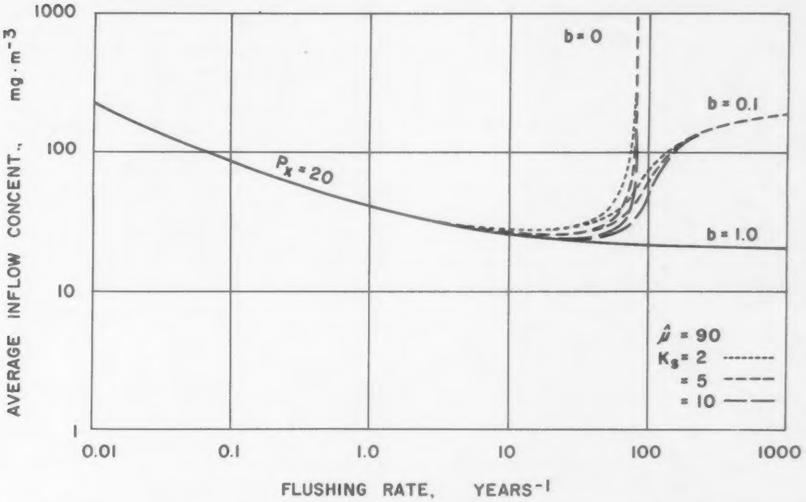

FIG. 5. Sensitivity analyses showing the effect of the half-saturation constant on calculated values of in-lake cellular P when 0, 10, and 100% of the inflowing P is in the cellular form.

Sensitivity Analysis

To solve the model equations, it was necessary to specify values for certain key parameters. In particular, we used values of 0.25 d^{-1} (90 yr^{-1}) for the maximum specific growth rate and 5 $mg \cdot m^{-3}$ for the half-saturation constant in the previous examples. Because these numbers might be subject to debate, we conducted a sensitivity analysis to investigate model responses to numerical changes in the parameters $\hat{\mu}$ and K_s.

For this analysis, we selected values which represent reasonable range for the two parameters which might be expected in nature. Maximum specific growth rate was assigned values of 45, 90, and 180 yr^{-1} and K_s took on values of 2, 5, and 10 $mg \cdot m^{-3}$.

To simplify the results of the $\hat{\mu}$ analysis, we plotted only lines of $P_x = 20$ for values of $b = 0$, 0.1, and 1.0 (Fig. 4). Figure 4 shows that the model is sensitive to $\hat{\mu}$ in the range $\hat{\mu}/10 > \rho > \hat{\mu}$, but is insensitive to this parameter at lesser flushing rates. Beginning with the plot for $b = 0$, $\hat{\mu}$ plays a predominate role in determining the flushing rate at which washout occurs: for extreme levels of P_0, ρ_w approaches $\hat{\mu} - \sqrt{\mu}$ as a limit. For $b = 0.1$, the sensitivity is decreased although it is still significant. The model is insensitive to $\hat{\mu}$ when $b = 1.0$ because all incoming P is bound in algal cells and none is available for growth. In general, the model is sensitive to $\hat{\mu}$ when the flushing rate exceeds $\hat{\mu}/10$, but that sensitivity decreases as b increases.

Figure 5 shows the plots for the K_s analysis for $P_x = 20$ with $b = 0$, 0.1, and 1.0. The model results are much less sensitive to changes in K_s than to changes in $\hat{\mu}$. Furthermore, the impact occurs over a much narrower range of flushing rates. For example, for $b = 0.1$, the model is sensitive to K_s between flushing rates of approximately 10 and 200 yr^{-1}. As with the $\hat{\mu}$ analysis, it can be shown that model sensitivity decreases with increasing b. At $b = 1.0$, model results are insensitive to changes in K_s, since no P is available for growth.

In summary, the sensitivity analysis indicates that the model is sensitive to the algal growth parameters $\hat{\mu}$ and K_s only for flushing rates greater than $\hat{\mu}/10$. Furthermore, we showed that the percentage of P_0 that is in algal cells also significantly influences sensitivity, with sensitivity decreasing as b increases. Quantitatively, the specific value of $\hat{\mu}$ is much more critical than is K_s: given the general nature of the model, any reasonable value of K_s should suffice. The maximum specific growth, however, is a critical parameter and even though we do not view the model as having specific quantitative predictive capabilities, the correlation of model results with natural systems would be significantly enhanced by a more rigorous determination of $\hat{\mu}$. Future work should focus more closely on ways to estimate this parameter.

The specific results depicted in Fig. 1, 2, and 3 are based on the parameters $\hat{\mu} = 90\ yr^{-1}$ and $K_s = 5\ mg \cdot m^{-3}$. We consider these values to be reasonable, but at the same time, we are uncertain of the extent to which results obtained with these values are applicable to natural systems. The information presented in Fig. 1–3 should be interpreted qualitatively: it is clearly beyond the resolution of our analysis to suggest that lakes having an average input concentration of 100 $mg \cdot m^{-3}$ would exhibit cellular reduction at a flushing rate of 50 yr^{-1} and that washout would occur at 80 yr^{-1}. However, we suggest that lake managers should be aware that cellular reduction and washout can occur at flushing rates of this general range and the implications should be weighed carefully in management decisions. Also, since algal species grow at different rates, high flushing rates might be expected to cause a restructuring of algal populations rather than a uniform reduction in all species. Fortunately, nuisance blue-greens tend to have lower maximum specific growth rates than greens or diatoms (Zison et al. 1978) and therefore, blue-greens might be reduced most by high flushing rates. On the other hand, periphyton and rooted aquatic plants are not subject to washout, so that problems due to excessive plant growth are possible even though populations of pelagic algae may be reduced.

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The Effect of Production Variability on Financial Risks of Freshwater Prawn Farming in Hawaii[1]

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Samples, K. C., and P. S. Leung. 1985. The effect of production variability on financial risks of freshwater prawn farming in Hawaii. Can. J. Fish. Aquat. Sci. 42: 307–311.

A conceptual model of a stochastic production process is proposed which illuminates the business perils associated with shortfalls in yields of aquacultured freshwater prawns. Commercial production data are statistically analyzed within the context of the model to measure the extent to which yield variability engenders financial risks for prawn producers. It is shown that at wholesale prawn prices of US$11.00/kg there is a 50% probability that a representative 8-ha prawn farm utilizing ponds greater than 0.8 surface ha will incur a financial loss in any given year. This probability falls to 30% when ponds smaller than 0.4 surface ha are utilized.

On présente un modèle conceptuel d'un processus stochastique de production qui fait ressortir les dangers financiers découlant de mauvais rendements en élevage de la crevette d'eau douce. Les données de la production commerciale font l'objet d'une analyse statistique dans le cadre du modèle dont le but est de déterminer dans quelle mesure la variabilité de la production est source de risques financiers pour les producteurs de crevettes. On montre que, au prix de gros de 11$ US le kilogramme de crevettes, il y a 50 % de probabilité qu'une installation de production de crevettes représentative (8 ha, avec étangs de superficie supérieure à 0,8 ha) subira une perte financière au cours d'une année donnée. Cette probabilité tombe à 30 % si l'on utilise des étangs de superficie inférieure à 0,4 ha.

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Inquiries into aquaculture production economics have typically focused on quantifying expected financial performance of alternative production systems. In most instances, scant attention appears to have been devoted to examining the extent to which actual financial performance levels diverge from expected levels because of unforeseen variations in market prices and production yields. Consequently, little is formally understood about the degree of financial risk exposure in commercial aquaculture. The purpose of this paper is to begin to explore the relationship between yield variability and financial risk in freshwater prawn (*Macrobrachium rosenbergii*) aquaculture. A conceptual model of a stochastic production process is proposed which illuminates the business perils associated with unplanned downturns in aquaculture yields. Historical freshwater prawn production data are then analyzed within the context of the model to determine whether yield variability engenders financial risks for prawn producers in Hawaii.

Yield and Profit Variability

Considerable effort has been devoted to exploring the economic ramifications of stochastic production processes including contributions by Horowitz (1970), Roumasset (1976), Richardson and Mapp (1976), Richardson and Condra (1981), among others. Although not specifically concerned with aquaculture, these authors have modeled and measured the relationship between agricultural yield variability and financial risks. The basis of the relationship rests wholly on the manner in which alternative yield amounts per hectare (q) influence farming profitability. Let annual profit per surface hectare in prawn production (P) be expressed as the difference between annual operating revenues and costs per hectare:

$$(1) \quad P = p \cdot q - \{c(w, q) + s \cdot q\}$$

where the scalar p and vector w represent exogenously determined output and input prices, respectively; $c(w, q)$ is the total preharvest cost of producing q, where $c(w, q)$ is nondecreasing in w and q; and the scalar s denotes the per unit cost associated with harvesting and selling prawn products. Expected profit per hectare is therefore given by $E(P) = pE(q) - \{c(w, E(q)) + sE(q)\}$. When actual harvest levels are less than anticipated (i.e. $q < E(q)$), realized profits deviate from $E(P)$ by a factor equal to

$$(2) \quad E(P) - P = (p - s) \cdot \{E(q) - q\} - \{c(w, E(q)) - c(w, q)\}.$$

The degree to which realized profitability deviates from its expected level depends on the sensitivity of operating revenue and costs to output fluctuations. Looking first at revenues, when q falls below its expected level, a decline in sales typically occurs, the amount of which depends on the response of prices to output reductions. If output prices are constant ($dp/dq = 0$), revenues per hectare will unambiguously decline in exact proportion to the harvest reduction. However, when there are numerous operators who together suffer similar crop failures, output prices may be bid up by buyers in response to perceived market shortages. The direction and magnitude of the revenue impact due to a yield downturn would in this case be uncertain.

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[2] Senior authorship not assigned.

Unforeseen reductions in prawn yields from expected levels may also affect operating costs. For instance, a reduction of certain expenses associated with harvesting, storing, and selling farm output is generally observed. On the other hand, preharvest production costs which arise from nurturing the crop to maturity such as feed, labor, or electricity expenses will already be encumbered if the yield diminution is unplanned. This is typically the case in outdoor pond prawn production systems. Frequently, heavy algal blooms are maintained to provide shelter for prawns, and to supply nutrients to pond organisms at the base of the food chain. The presence of algae drastically reduces visibility and makes it difficult to monitor changes in prawn biomass. Although production sampling methods have been developed (Huang et al. 1976), most producers tend to treat their ponds as "black boxes" and apply feed and water inputs according to a predetermined production formula. Consequently, a significant portion of variable costs is sunk by the time a production shortfall is discovered. Fixed operating costs including debt service charges, depreciation, insurance, administrative overhead, and certain utility expenses also remain unchanged if $q < E(q)$.

The combined effect of a random reduction in yields on profitability is quite predictable if output prices are insensitive to production levels, and production inputs are administered on a predetermined formula basis. When preharvest input levels are fixed such that $c(w, q) = C$, where C is a constant, then the last term of equation (2) can be ignored. Since the term $p(E(q) - q)$ is positive and larger than $s(E(q) - q)$ because $p > s$, equation (2) is strictly positive in instances where $q < E(q)$. The opposite is true where $q > E(q)$.

Given the direct interaction between profits and realized yield levels, a relationship between the variances of yield and profit per hectare can be derived. From equation (1), and assuming $c(w, q) = C$, it can be seen that after simplification, variance in profit per hectare is given by

$$(3) \quad V(P) = (p - s)^2 V(q).$$

It follows that $dV(P)/dV(q) > 0$, provided that $p \neq s$. Fluctuations in yields and profits are of consequence to commercial aquaculturalists when the probability is high that operating profits will fall below some minimally acceptable level P^* (Fishburn 1977; Menezes et al. 1980). The chance of this occurring depends on the probability that $q < q^*$, where q^* is implicitly defined such that $P^* = p \cdot q^* - \{c(w, q^*) + s \cdot q^*\}$. Figure 1 illustrates this phenomenon. The probability that aquaculture yields will fall below q^* due to random natural events is indicated by the shaded area in Fig. 1a. Associated directly with this probability is the corresponding probability that profit per hectare will fall below P^*. The chance of such an occurrence is illustrated by the shaded area in Fig. 1b.

Financial Risks in Freshwater Prawn Farming

Commercial aquaculture production of freshwater prawns has expanded significantly on a worldwide basis during the last decade. In Hawaii, where environmental conditions are particularly favorable to prawn husbandry, area in *Macrobrachium* production increased from 0.6 ha in 1970 to 103 ha in 1983. In 1983, total industry production levels reached 122 000 kg, valued at about US$1.4 million. However, during the recent history of freshwater prawn aquaculture development in Hawaii, several commercial operations including a 40-ha farm terminated operations due to unexpectedly low production yields.

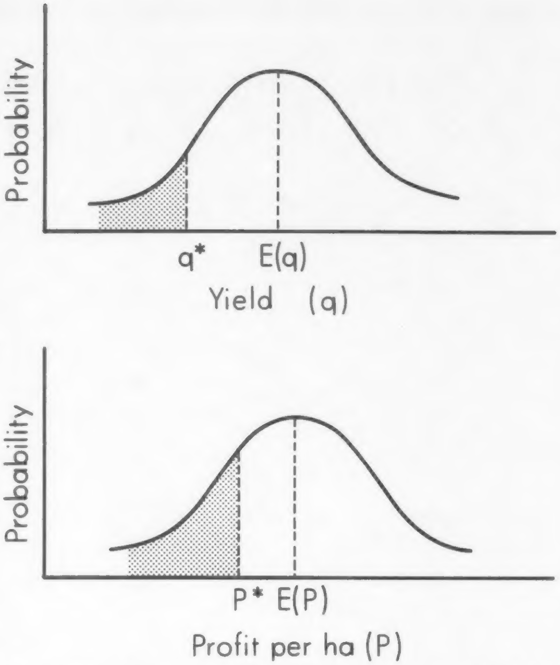

FIG. 1. Hypothetical probability distributions for yield and profit per hectare.

Historical freshwater prawn production data for the years 1975–81 were obtained from the "Prawn Harvesting/Stocking Data System" maintained by the Department of Animal Science at the University of Hawaii. The data system includes time series observations of harvest quantities for various ponds located throughout the state. Stocking rate data are also available, but they are incomplete. Twenty farms participating in the data collection system represented about 95% of the commercial prawn farm population and were responsible for 50% of Hawaii's total annual freshwater prawn production during the period 1975–81. Hawaii's largest prawn farming operation was not included in the sample group. Only 4 of the 20 farms were operated on a full-time basis. The size of the participating farms ranged from 0.1 to 10 surface ha. Cross-sectional and time series data on pond output levels were pooled and a total of 191 observations of annual yield (kilograms per hectare per year) were available for further empirical study. Use of time series data accounted for the effects of random events such as weather variability on yields. Cross-sectional observations drawn from different farms accounted for yield variation due to differences in pond location and size, and management practices. Yield variation within and across farms was therefore captured using the pooled data. Sizes of individual pond included in the sample ranged from 0.08 to 1.54 surface ha. For analytical purposes, pond observations were classified into three size (surface) categories: (I) less than 0.4 ha ($N = 66$); (II) 0.4–0.8 ha ($N = 78$); and (III) larger than 0.8 ha ($N = 47$). This

TABLE 1. Summary of statistical tests concerning the normality of freshwater prawn yields.

Pond size[a]	Sample size	Mean	Standard deviation	D-statistics[b]	Probability level[c]	Skewness G1	Probability level[c]	Kurtosis G2	Probability level[c]
I	66	2308	878	0.139	0.01	1.105	0.000	0.744	0.201
II	78	2038	585	0.130	0.01	1.432	0.000	4.853	0.000
III	47	1813	523	0.170	0.01	1.976	0.000	5.214	0.000

[a] I = less than 0.4 ha; II = 0.4–0.8 ha; III = greater than 0.8 ha.
[b] Kolmogorov–Smirnov statistics.
[c] Significance level of immediately preceding statistics.

TABLE 2. Summary of statistical tests concerning the lognormality of freshwater prawn yields.

Pond size[a]	Sample size	D-statistics[b]	Probability level[c]	Skewness G1	Probability level[c]	Kurtosis G2	Probability level[c]
I	66	0.064	0.20	0.269	0.362	−0.325	0.576
II	78	0.078	0.20	−0.113	0.678	1.317	0.014
III	47	0.116	0.15	0.932	0.007	1.519	0.026

[a] I = less than 0.4 ha; II = 0.4–0.8 ha; III = greater than 0.8 ha.
[b] Kolmogorov–Smirnov statistics.
[c] Significance level of immediately preceding statistic.

enabled investigations to be made into whether pond size influences yield variability, a contention made elsewhere by Huang et al. (1976) and Gibson and Wang (1977).

Prawn yields were first hypothesized to be normally distributed. The Kolmogorov–Smirnov goodness-of-fit test was used to test the prawn yield data against the normal distribution (Winkler and Hays 1971). The test was performed on yields for all three pond size categories. Fisher's *G*-statistics (G1 and G2) and their respective significance levels were also computed for each pond size category as supplemental tests to detect departure from normality (Fisher 1970). G1 is a measure of the amount of skewness, while G2 is a measure of kurtosis. For the normal distribution, $G1 = 0$ and $G2 = 3$.

The Kolmogorov–Smirnov *D*-statistics for all pond sizes exhibited a probability level (*p* value) of 0.01 (Table 1). Thus, at the 0.05 significance level, the null hypothesis of normality was rejected. In addition, the test for skewness provided evidence strongly suggesting that the distribution of prawn yields is asymmetric for all pond sizes. Tests for kurtosis also indicated nonnormal peakedness in all ponds except the small pond size category. Furthermore, G1 (skewness) statistics for all pond sizes indicated that the probability distributions of yields are positively skewed.

Viewed together, these findings suggests that prawn yields may be distributed lognormally rather than normally. The lognormal distribution of a random variable is positively skewed with the bulk of the probability falling into the lower range of possible values. Very little probability is associated with intervals containing only extremely high values of the variable in question. Furthermore, the mean is generally greater than the median for the lognormally distributed random variables, and the distribution also exhibits more peakedness than the normal distribution.

By transforming yield data to their natural logarithms, tests of lognormality could be conducted with precisely the same tools used above to test normality hypotheses (Table 2). At the 0.05 significance level, the null hypothesis of lognormality could not be rejected, regardless of pond size.

Further analyses were performed to test the equality of means and variances of the logarithmic-transformed yields across the three subsamples representing different pond sizes. One-way analysis of variance indicated that subsample means are significantly different from one another with a *p* value of 0.0038. Bartlett's test of variance homogeneity showed that the variances are different across the three pond size subsamples with a *p* value of 0.0166. Pairwise tests of variance homogeneity were also performed with no indications of homogeneous variances. In fact, a simple variance component analysis indicated that 15.12, 16.56, and 68.21% of annual yield variability is attributed to year-to-year variations, pond size variations, and unknown random disturbances, respectively. Based on these combined findings it was decided to treat the three pond sizes separately for risk assessment purposes.

Using the probability structure of prawn yields suggested by historical data, it is a straightforward exercise to derive analytically the probability density function for profits stemming from prawn farming in Hawaii. In so doing, it is possible to calculate explicitly the probability that annual operating profits per hectare will fall below some specified minimal profit level P^*. This can be accomplished by first simplifying equation (1) as

$$(4) \quad P = pq - c$$

where c represents the total annual per hectare cost associated with prawn farming in Hawaii. For purposes of risk analysis, costs are treated as deterministic and independent of final realized yields. In view of the peculiar "black box" prawn production phenomenon in Hawaii, this is quite reasonable given the fact that almost all of production costs are incurred before actual output levels are determined through harvesting. Prawn farming cost/return data reported by Shang (1981) show that 42% of the operating costs for an 8-ha farm are overhead costs. These include costs for rent, debt service, property taxes, and insurance, which do not vary with production output. Labor contributes another 27% to total costs. For all practical purposes, labor costs are tied to expected output levels rather than actual yields. Workers generally enjoy steady employment on prawn farms as long as operations continue. Some farms employ additional workers for harvesting. This is only because harvesting using seine nets is labor intensive, regardless of how many prawns are finally captured. Feed costs represent 18% of total costs. As mentioned above, prawns are routinely fed at various recommended rates depending on their maturity. Daily feed rations can be decreased if uneaten food is evident. However, normal pond conditions limit the effectiveness of this feed control practice. When other cost items such as juveniles are considered, over 95% of total operating costs are sunk by the time harvesting occurs.

Due to lack of empirical data on the matter, it is assumed that annual costs are not influenced by pond size. Although unexplored, it is suspected that pond size probably affects construction costs, and thereby influences annual depreciation costs. Pond size may also affect labor expenses associated with feeding and harvesting.

Given lognormally distributed prawn yields, it follows from equation (4) that

$$(5)\quad \begin{aligned}\Pr[P \leqslant P^*] &= \Pr[(pq - c) \leqslant P^*]\\ &= \Pr[q \leqslant ((P^* + c)/p)]\\ &= \Pr[x \leqslant \ln((P^* + c)/p)]\\ &= \Pr\left[z \leqslant \frac{\ln(P^* + c)/p) - m}{\sigma}\right]\end{aligned}$$

where $x = \ln q \sim N(m, \sigma^2)$ and z = standard normal variate ~ $N(0, 1)$. Using this information, along with an estimated annual operating cost (c) for an 8-ha farm of US$7829/0.4 ha (Shang 1981), and selling price (p) of US$11.00/kg, the probability levels of incurring a loss ($\Pr[P \leqslant 0]$) can be calculated for each pond size category. These probabilities are 0.298, 0.356, and 0.507 for pond sizes I, II, and III, respectively. Estimated probabilities of losses occurring at selling prices ranging from US$8.80 to US$17.63/kg are given in Table 3 for the three different pond sizes. These prices reflect the general range of selling prices available to prawn producers.

It is apparent that farms using smaller ponds generally face reduced probabilities of incurring financial losses than those with larger ponds. As shown in Table 3, this result is consistently evident when comparing pond sizes I and III, regardless of selling price. However, by the nature of statistical properties of lognormal distributions, estimated probabilities of incurring losses become less disparate between pond sizes at increasingly higher selling prices. Furthermore, due to the differing degrees of skewness of the probability distributions for alternative pond sizes, it happens that the relative riskiness of using one pond size versus another may change as selling prices increase. Consequently, at selling prices of US$17.63 or higher, farms utilizing pond size I face the highest probabilities of incurring financial losses.

TABLE 3. Probability that a representative 8-ha freshwater prawn farm in Hawaii will incur a financial loss in any given year.

	Prawn selling price ($US/kg)				
Pond size	8.80	11.00	13.22	15.43	17.63
I (less than 0.4 ha)	0.523	0.298	0.157	0.078	0.038
II (0.4–0.8 ha)	0.655	0.356	0.161	0.066	0.024
III (greater than 0.8 ha)	0.805	0.507	0.252	0.104	0.039

Concluding Remarks

Randomness in aquaculture production engenders the risk that the financial performance of a particular commercial aquaculture operation will not meet minimal performance requirements during any given period. The extent of this risk can be empirically evaluated if the probability density function of yields is known, or can be estimated, and if production costs and returns are sufficiently well understood.

In the case of freshwater prawn farming in Hawaii, random elements such as weather, disease, water quality, and natural food availability combine to create variation in annual harvests. Commercial freshwater prawn yields reported by 20 farms appear to be distributed lognormally, indicating that there exists relatively high probabilities that actual yield for any randomly selected pond and period will be less than average. This finding, when combined with what is currently known about prawn production costs and returns, suggests that commercial prawn aquaculturalists in Hawaii face significant risks that farm revenues will not adequately cover accrued production costs. Two important qualifications must be made regarding the conclusion. First, data limitation on the relationship between production costs and yields does not permit a complete analysis of the financial risk situation. If production shortfalls can be anticipated, and inputs such as feed reduced accordingly, then the probability of a financial loss would be less than predicted above. The probability estimates reported here also do not account for the link between yield variation and the costs of utilizing risk-augmenting or risk-reducing production inputs. For example, use of low-quality budget feeds may increase yield variability. Conversely, investment in costly automatic monitoring devices and pond environment control mechanisms may reduce yield variability. A general lack of understanding about the economics of production control puts limitations on empirical assessments of prawn farming financial risks. A second qualification relates to a potential sampling bias. Available prawn yield data reflect production circumstances in small part-time farms. If farm size is related to sophistication in production management, large farms may exhibit less yield variability than the farms sampled here. If so, financial risks faced by investors in large freshwater prawn farming operations are less than those stated above.

The extent of financial risk in freshwater prawn aquaculture appears to be sensitive to the average price received for farm output and the average size of ponds used in prawn production. For any given pond size, the probability of incurring a financial loss in any year declines dramatically as average selling price increases from US$8.80 to US$17.63/kg. At a selling price of US$8.80/kg, there is at least a 50% probability that a representative 8-ha farm will incur a loss regardless of pond size. This probability drops to less than 5% when average selling price reaches US$17.63/kg.

This paper is a first step towards an empirical understanding of financial risks in commercial aquaculture. Future research on yield variation should look more closely at the influence of different cultural practices on output variability. In many instances, yield variation is subject to control. However, more research is needed to identify cost-effective ways of achieving production control. Further research on price variability and its impact on financial risk is also needed. Price variation was not addressed in this study. Nevertheless, random changes in output prices may generate as much uncertainty for aquaculturalists as stochastic production processes.

Acknowledgements

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Variation in Length and Body Depth of Pink Salmon (*Oncorhynchus gorbuscha*) and Chum Salmon (*O. keta*) in Southern British Columbia

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Beacham, T. D., and C. B. Murray. 1985. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 312–319.

The magnitude of within-stock variability of postorbital–hypural length and body depth was investigated for spawning pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) stocks. Variability of postorbital–hypural length and body depth of male pink salmon, all maturing at 2 yr of age, was greater than that for male chum salmon, maturing at ages of 3–5 yr. Female pink salmon were less variable for the two characters than all ages of female chum salmon, equally variable when only age 3 or age 4 female chum salmon were considered, and more variable in comparison with age 5 female chum salmon. Males were more variable for each character than females for both species. Small males of both species tend to resemble females when body depths are compared. It is suggested that small males mimic females to reduce aggression from larger males and gain access to spawning females.

L'importance de la variabilité, au sein du stock, de la distance entre les os postorbitaire et hypural, et de la hauteur du corps, a été étudiée chez des saumons roses (*Oncorhynchus gorbuscha*) et des saumons kétas (*O. keta*) en période de fraie. La variabilité de ces deux paramètres chez des saumons roses mâles tous matures à 2 ans était supérieure à celle de saumons kétas mâles, matures entre 3 et 5 ans. Ces deux paramètres étaient moins variables chez les femelles de saumon rose comparativement aux femelles de saumon kéta de tous âges, mais également variables si l'on ne tenait compte que des âges 3 ou 4 et moins variables si l'on ne tenait compte que des femelles d'âge 5. Dans les deux espèces, chacun des paramètres était plus variable chez les mâles que chez les femelles. Les petits mâles de chacune des espèces presentaient une ressemblance avec les femelles pour ce qui est de la hauteur du corps. On émet l'hypothèse que la ressemblance entre les petits mâles et les femelles a pour but de réduire l'agression par les gros mâles et de permettre aux premiers d'atteindre les femelles en fraie.

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Age and size at return to the natal spawning grounds is variable for Pacific salmon. Precociously maturing males or "jacks" are regularly found as part of the spawning population for sockeye salmon (*Oncorhynchus nerka*) (Hanson and Smith 1967; McCart 1970), coho salmon (*O. kisutch*) (Shapovalov and Taft 1954; Gross 1983), and chinook salmon (*O. tshawytscha*) (Robertson 1957; Gebhards 1960). These males are considerably smaller than other spawning males. Coho salmon jacks return to spawn during the year in which they migrated to the ocean, whereas chinook and sockeye salmon jacks spend one winter in the ocean. These jacks are not large enough to defend females from other larger males, but instead function as "satellite" males (Hanson and Smith 1967), sneaking in to the territory of a dominant male and female during spawning and attempting to fertilize some of the female's eggs.

Pink salmon (*O. gorbuscha*) mature at 2 yr of age (Bilton and Ricker 1965), and jacks are not present in spawning populations. Chum salmon (*O. keta*) return to spawn in British Columbia mainly at 3–5 yr of age (Ricker 1980; Beacham and Starr 1982), with age 2 males exceptionally rare (Pritchard 1943; Beacham et al. 1983). The smaller males tend to function as "satellite" males in spawning chum salmon populations (Schroder 1981) and in pink salmon populations (Chebanov 1980).

Male Pacific salmon develop a dorsal hump during maturation and spawning as a secondary sexual characteristic. This hump is most prominent in pink salmon, which are known alternatively as "humpback," and it is probably the most pronounced sexually dimorphic character (Davidson 1935). However, it is uncertain if hump size develops proportionately in all males, though it is particularly conspicuous in large individuals (Smirnov 1975).

Body size is of considerable importance in determining a male's access to spawning females in Pacific salmon (Chebanov 1980; Schroder 1981; Chebanov et al. 1983). Variability of male size in a species that matures at several ages should be greater than within a species where all males mature at the same age. If smaller males have restricted access to spawning females, an alternative mating strategy for small males might be to reduce the visibility of their sexually dimorphic characters in order to reduce aggression from larger males, and possibly

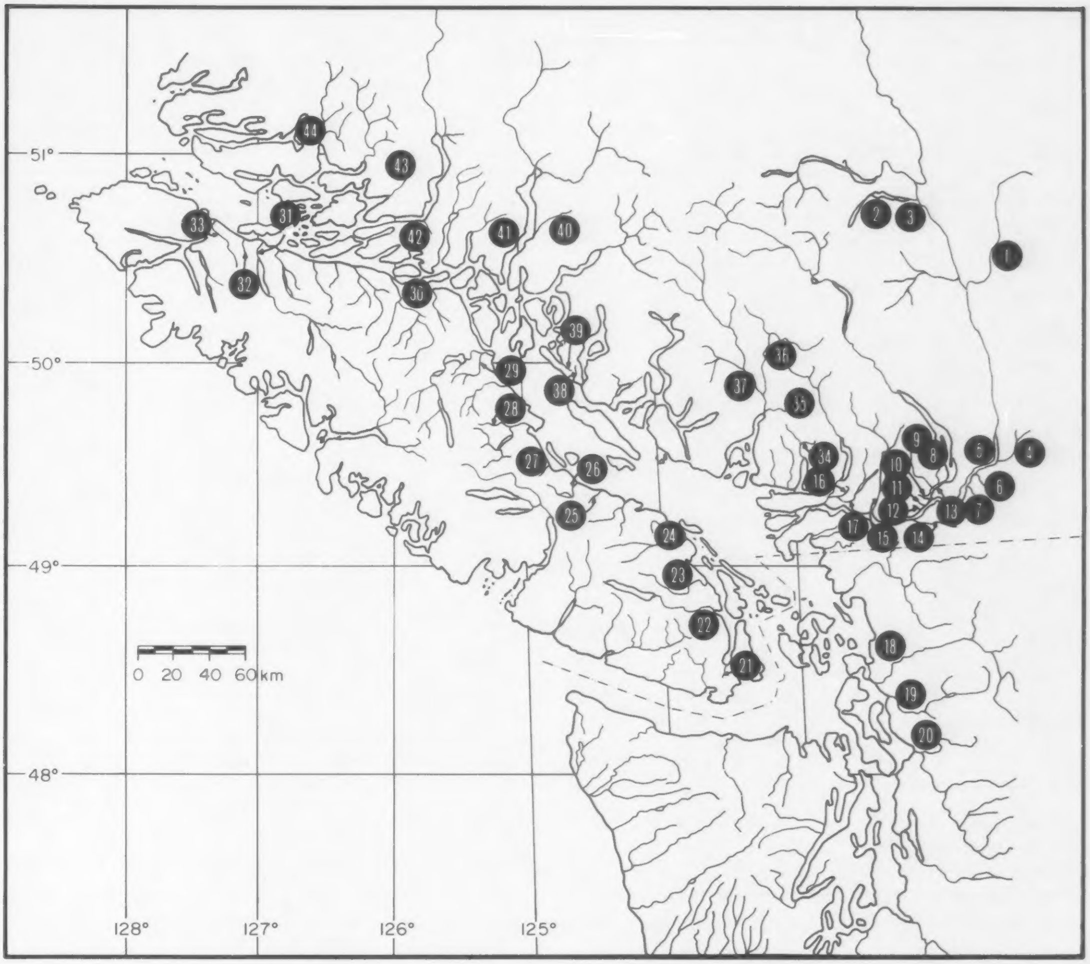

FIG. 1. Locations of rivers where pink and chum salmon stocks were sampled in British Columbia and Washington. Rivers, listed in ascending order: (1) Thompson, (2) Portage, (3) Seton, (4) Coquihalla, (5) Fraser, (6) Jones, (7) Wahleach, (8) Weaver, (9) Chehalis, (10) Squakum, (11) Inch, (12) Chilqua, (13) Harrison, (14) Vedder, (15) Stave, (16) Blaney, (17) Alouette, (18) Skagit, (19) Stillaguamish, (20) Snohomish, (21) Goldstream, (22) Cowichan, (23) Chemainus, (24) Nanaimo, (25) Little Qualicum, (26) Big Qualicum, (27) Rosewall, (28) Puntledge, (29) Quinsam, (30) Adam, (31) Nimpkish, (32) Cluxewe, (33) Keogh, (34) Indian, (35) Mamquam, (36) Cheakamus, (37) Squamish, (38) Sliammon, (39) Okeover, (40) Orford, (41) Phillips, (42) Kakweiken, (43) Glendale, (44) Wakeman.

maintain position near a spawning female. We investigated these topics by examining the variance and degree of sexual dimorphism in body length and body depth of spawning pink and chum salmon populations in southern British Columbia.

Methods and Materials

Pink salmon were sampled on spawning grounds in 1982 and 1983, and chum salmon during 1981 to 1983 (Fig. 1). Samples were taken during the later portions of the spawning period so that all individuals sampled were fully mature. All salmon in this study were collected with beach seines or by sampling fresh dead fish. Full details of the 1981 and 1982 chum salmon sampling were outlined by Beacham et al. (1983). Similar procedures were followed for the 1982 pink salmon and 1983 pink and chum salmon collections. Postorbital–hypural length (Vladykov 1962) for each individual was recorded with a measuring stick to the nearest millimetre, and body depth (Hubbs and Lagler 1958) was recorded with calipers to the nearest millimetre. Body depths of females were recorded only on fish that had completed spawning. Ages of chum salmon were determined from scales as outlined by Bilton and Ricker (1965) and LaLanne and Safsten (1969). All pink salmon were asssumed to be 2 yr old (Bilton and Ricker 1965; Aspinwall 1974). The sex of each individual measured was confirmed by internal inspection.

Variation in postorbital–hypural length and body depth was determined separately for each sex and partitioned into two components: between-stock and within-stock variation. For each sex, a one-way analysis of variance was conducted with stock as the only source of variation. The within-stock variation for each character was estimated as the standard deviation of

TABLE 1. Mean postorbital–hypural length (mm), standard deviations, ranges, % difference in size between smallest and largest individual, and coefficient of variation (%) for even- and odd-year pink salmon stocks in southern British Columbia.

	Male						Female					
Stock	*N*	Mean	SD	Range	(Max − min)/min (%)	CV	*N*	Mean	SD	Range	(Max − min)/min (%)	CV
Even-year stocks												
Glendale	67	363.4	35.6	292, 453	55	9.8	32	390.0	19.1	354, 433	22	4.9
Cluxewe	44	388.8	33.4	310, 451	45	8.6	33	375.8	20.0	310, 410	32	5.3
Quinsam	50	389.0	26.7	323, 444	37	6.9	50	387.3	18.3	343, 433	26	4.7
Puntledge	8	374.9	26.8	339, 417	23	7.1	49	377.4	19.4	332, 426	28	5.1
Odd-year stocks												
Glendale	59	402.6	28.2	355, 480	35	7.0	41	406.6	15.6	380, 460	21	3.8
Quinsam	50	427.8	31.9	370, 532	44	7.5	50	402.5	15.8	364, 442	21	3.9
Puntledge	4	392.0	5.0	385, 396	3	1.3	96	402.2	21.3	344, 470	37	5.3
Skagit	51	432.7	30.3	359, 497	38	7.0	51	409.9	17.0	378, 452	20	4.1
Snohomish	47	430.1	23.2	376, 472	26	5.4	55	409.9	16.1	363, 449	24	3.9
Stillaguamish	59	450.0	29.9	387, 498	29	6.6	59	423.3	17.5	392, 463	18	4.1
Phillips	52	400.4	24.8	350, 451	29	6.2	48	407.3	18.6	369, 444	20	4.6
Keogh	66	393.5	22.2	352, 466	32	5.6	34	396.3	13.9	370, 417	13	3.5
Adam	68	407.3	30.9	324, 484	49	7.6	32	388.9	21.4	349, 450	29	5.5
Indian	74	419.5	33.5	350, 485	39	8.0	26	411.2	21.0	373, 465	25	5.1
Kakweiken	53	419.9	28.7	357, 487	36	6.8	47	409.6	12.8	376, 438	16	3.1
Wakeman	61	411.3	43.9	332, 496	49	10.7	39	404.3	20.0	365, 440	21	4.9
Jones	64	424.9	26.4	377, 518	37	6.2	36	406.4	27.0	332, 490	48	6.6
Coquihalla	33	416.8	33.1	329, 477	45	7.9	67	412.7	22.8	315, 480	52	5.5
Fraser	84	454.0	26.4	390, 513	32	5.8	116	426.5	21.8	370, 480	30	5.1
Vedder	91	456.9	24.8	396, 506	28	5.4	109	433.9	22.2	379, 491	23	5.1
Harrison	102	459.8	30.6	384, 536	40	6.7	98	435.6	25.1	360, 500	28	5.8
Thompson	59	451.0	31.8	370, 511	38	7.1	141	422.0	23.0	363, 475	24	5.5
Seton	95	430.6	30.8	371, 515	39	7.2	105	424.5	21.5	377, 486	29	5.1
Portage	41	432.5	22.5	398, 495	24	5.2	59	416.9	18.1	385, 465	21	4.3

the residual mean square. Chum salmon were also separated according to their age of return for each sex. A one-way analysis of variance with stock as the sole source of variation was conducted for each age and sex combination. Within-stock variation was again estimated as the standard deviation of the residual mean square.

Postorbital–hypural lengths and body depths were also log-transformed to reduce the correlation of the means and variances (Sokal and Rohlf 1969), similar to Handford's (1980) study on morphological variability in sparrows, *Zonotrichia capensis*. One-way analysis of variance with stock as the sole source of variation was again conducted in order to estimate the within-stock variance for postorbital–hypural length and body depth. Tests of equality of within-stock variances of body length and body depth were conducted with variances derived from the log-transformed variables. Similar tests could also be conducted on the untransformed variables by comparing the coefficients of variation, the procedure being outlined by Sokal and Braumann (1980).

We examined whether or not all males and females were distinctively sexually dimorphic based upon their body length and depth. We used discriminant analysis to classify salmon as to their sex based solely upon an individual's length and body depth. Once we determined which individuals were correctly classified and which were misclasssified for each stock, we used a two-way analysis of variance with stock and classification (correct or incorrect) as the indices to compare mean lengths of those individuals that were correctly classified with those that were misclassified. This analysis was conducted for each sex for which both body length and body depth were recorded.

Results

Postorbital–Hypural Length

Male pink salmon were generally larger and more variable in length than were females (Table 1). The largest males sampled in a stock were usually 30–50% (mean 37%) greater in length than the smallest males sampled. The largest females were 20–30% (mean 26%) greater in length than the smallest females. The coefficient of variation of length for males (excluding Puntledge) ranged from 5.2 to 10.7%, whereas that for females ranged from 3.1 to 6.6%. Pink salmon in the odd-year stocks were larger than those in the even-year stocks. Within a stock, male pink salmon were clearly more variable in length than females for both even-year ($F = 2.90$; df = 165, 160; $P < 0.01$) and odd-year stocks ($F = 1.99$; df = 1193, 1289; $P < 0.01$). Male pink salmon, all maturing at 2 yr of age, were also relatively more variable in length than male chum salmon, maturing from 3 to 5 yr of age (Table 2). This result was apparent for both even-year ($F = 2.04$; df = 165, 1916; $P < 0.01$) and odd-year ($F = 1.34$; df = 1193, 1916; $P < 0.01$) pink salmon stocks. Males in a spawning population of pink salmon were also more variable in length than males of a specific age in a spawning chum salmon population.

Spawning male chum salmon were generally larger than spawning females in the same stock (Table 3). The largest males were generally 20–45% (mean 30%) greater in length than the smallest spawning males. The largest females were 20–35% (mean 29%) greater in length than the smallest females. The coefficients of variation of length for males ranged from 3.0 to 7.9%, and that for females from 3.7 to 7.1%. When all female

TABLE 2. Mean postorbital–hypural length (mm), body depth (mm), within-stock standard deviation, coefficient of variation (%), within-stock variance of log-transformed lengths and body depths, and degrees of freedom for variance.

Sex	Age	Character	N	Mean	SD	CV	Variance	df
Even-year pink salmon								
Male	2	Length	169	378.1	32.2	8.5	0.00734	165
Female	2	Length	164	382.5	19.1	5.0	0.00253	160
Odd-year pink salmon								
Male	2	Length	1213	429.7	29.6	6.9	0.00481	1193
		Depth	1213	139.8	20.3	14.5	0.02030	1193
Female	2	Length	1309	417.9	20.6	4.9	0.00242	1289
		Depth	185	94.3	8.3	8.8	0.00796	181
Chum salmon								
Male	3	Length	540	556.9	28.7	5.2	0.00270	517
	4	Length	1203	596.7	29.8	5.0	0.00255	1176
	5	Length	200	611.5	29.1	4.8	0.00234	177
	All	Length	1943	585.6	34.7	5.9	0.00359	1916
	3	Depth	185	153.7	15.5	10.1	0.01023	174
	4	Depth	743	180.6	18.6	10.3	0.01121	727
	5	Depth	99	188.9	15.7	8.3	0.00710	85
	All	Depth	1027	176.8	19.8	11.2	0.01323	1011
Female	3	Length	442	545.0	25.6	4.7	0.00223	416
	4	Length	1339	582.3	29.4	5.0	0.00258	1312
	5	Length	179	602.8	26.0	4.3	0.00187	158
	All	Length	1960	575.3	32.9	5.7	0.00331	1933
	3	Depth	89	128.3	10.6	8.2	0.00716	81
	4	Depth	368	138.6	13.2	9.5	0.00911	359
	5	Depth	20	149.5	12.4	8.3	0.00647	12
	All	Depth	477	137.0	13.7	10.0	0.01027	468

chum salmon within a stock were considered as a single group, they were more variable in length than female pink salmon in both even ($F = 1.31$, $P < 0.01$) and odd years ($F = 1.37$, $P < 0.01$). When considered by age class, 3- and 4-yr-old female chum salmon were as variable in length as were female pink salmon. Pink salmon females in both even-year ($F = 1.35$, $P < 0.01$) and odd-year stocks ($F = 1.29$, $P < 0.01$) were more variable in length than 5-yr-old female chum salmon.

Male pink salmon were more variable in postorbital–hypural length than were females. When all ages of return were pooled within a spawning chum salmon population, males and females had similar variability in length ($F = 1.08$, $P > 0.05$) (Table 2). However, 5-yr-old chum salmon tended to be less variable in length than those 3 and 4 yr old, especially for females.

Body Depth

As Pacific salmon attain sexual maturity, the development of a dorsal hump, especially in pink and sockeye salmon, is a striking secondary sexual characteristic. For pink salmon sampled in the present study, body depth was a mean of 33% of postorbital–hypural length for males and 23% for females (Table 2). A regression of logarithm of body depth (BD) on logarithm of postorbital–hypural length (HL) yielded

$$\ln \mathrm{BD} = -4.19 + 1.50 \ln \mathrm{HL} \quad r = 0.74, N = 1213 \text{ males}$$

$$\ln \mathrm{BD} = 0.62 + 0.65 \ln \mathrm{HL} \quad r = 0.31, N = 185 \text{ females.}$$

Body depth increases more rapidly than length in male pink salmon but less rapidly in females. For pink salmon less than 350 mm postorbital–hypural length, the body depth of males was 27% greater than that of females, but for pink salmon between 441 and 470 mm in length, it was 59% greater (Table 4). Body depth is clearly more sexually dimorphic in larger pink salmon.

Male pink salmon had greater and more variable body depths than did females (Table 5). Coefficients of variation range between 9.9 and 21.4% for males and 6.3 and 11.7% for females for the stocks examined. The largest males had an average body depth 84% greater than the smallest males, whereas the largest body depth for females was an average of 48% greater than the smallest.

Male chum salmon, having a mean body depth of 30% of mean postorbital–hypural length (Table 2), have proportionately smaller humps than do male pink salmon. Female chum salmon had an average body depth of 24% of mean postorbital–hypural length, similar to that of female pink salmon. The regression of logarithm of body depth on logarithm of length yielded

$$\ln \mathrm{BD} = -4.54 + 1.52 \mathrm{\ HL} \quad r = 0.78, N = 1027 \text{ males}$$

$$\ln \mathrm{BD} = -4.28 + 1.45 \mathrm{\ HL} \quad r = 0.71, N = 477 \text{ females.}$$

Body depth again increases more rapidly in males than in females, but the sexual dimorphism is less marked than in pink salmon. Body depth of chum salmon less than 500 mm postorbital–hypural length was 17% greater for males than for females, but for chum salmon in excess of 650 mm in length, it was 22% greater (Table 4). Body depth is clearly not as sexually dimorphic in chum salmon as in pink salmon. Coefficients of variation for body length ranged from 7.6 to 15.0% for males and 8.2 to 13.1% for females (Table 6).

Body depth of male pink salmon within a stock was clearly

TABLE 3. Mean postorbital–hypural length (mm), standard deviations, ranges, % difference in size between smallest and largest individual, and coefficient of variation (%) for chum salmon stocks in southern British Columbia.

	Male						Female					
Stock	*N*	Mean	SD	Range	(Max − min)/min (%)	CV	*N*	Mean	SD	Range	(Max − min)/min (%)	CV
Weaver	65	555.0	41.2	450, 640	42	7.4	35	554.4	31.1	505, 620	23	5.6
Vedder	144	598.5	31.9	495, 680	37	5.3	156	579.9	30.6	490, 655	34	5.3
Harrison	141	590.5	46.4	472, 685	45	7.9	159	576.4	40.8	482, 675	40	7.1
Squakum	74	573.7	36.0	505, 683	35	6.3	51	568.5	33.0	485, 635	31	5.8
Inch	39	561.5	33.1	480, 631	31	5.9	61	554.0	36.2	485, 645	33	6.5
Blaney	49	582.5	39.0	515, 672	30	6.7	51	588.4	36.9	523, 670	28	6.3
Stave	26	589.4	29.7	520, 639	23	5.0	74	572.9	28.2	521, 656	26	4.9
Chehalis	117	579.4	33.9	486, 650	34	5.9	83	580.8	29.4	510, 645	26	5.1
Wahleach	42	586.4	28.4	530, 636	17	4.8	58	566.9	32.0	484, 630	30	5.6
Chilqua	49	542.8	32.0	479, 629	31	5.9	51	524.1	22.0	487, 573	18	4.2
Alouette	66	592.1	20.7	545, 640	17	3.5	34	581.6	29.9	505, 635	26	5.1
Nanaimo	17	605.9	29.3	550, 658	20	4.8	183	586.0	36.3	455, 690	52	6.2
L. Qualicum	160	588.8	34.8	490, 670	27	5.9	140	581.0	33.4	500, 665	33	5.8
B. Qualicum	128	598.2	41.5	465, 670	44	6.9	72	584.7	35.4	495, 655	32	6.1
Rosewall	57	559.8	27.4	504, 645	28	4.9	35	557.1	25.3	510, 596	17	4.5
Nimpkish	49	595.8	31.3	530, 691	30	5.3	38	575.3	21.5	530, 635	20	3.7
Sliammon	60	566.8	34.0	485, 634	31	6.0	40	570.8	33.2	489, 637	30	5.8
Cheakamus	74	623.6	28.2	565, 692	22	4.5	26	596.0	30.2	535, 645	21	5.1
Squamish	30	601.2	26.7	554, 660	19	4.4	70	594.3	34.6	508, 672	32	5.8
Mamquam	72	594.5	32.3	516, 674	31	5.4	29	577.5	39.9	494, 654	32	6.9
Okeover	46	547.6	31.3	480, 613	28	5.7	57	544.4	25.4	490, 620	27	4.7
Orford	51	604.2	32.4	523, 669	28	5.4	49	584.3	27.9	532, 645	21	4.8
Indian	16	627.4	18.8	609, 675	11	3.0	34	610.3	28.1	540, 660	22	4.6
Puntledge	102	593.3	34.6	471, 660	40	5.8	198	572.2	33.1	489, 644	32	5.8
Goldstream	55	579.0	36.2	441, 633	44	6.3	37	571.2	30.0	519, 640	23	5.3
Cowichan	118	593.0	30.3	500, 664	33	5.1	82	578.3	27.3	512, 650	27	4.7
Chemainus	96	566.8	38.4	475, 650	37	6.8	57	565.1	37.9	478, 660	38	6.7

TABLE 4. Mean body depth (mm) and mean postorbital–hypural length (mm) for spawning pink and chum salmon.

	Male			Female		
Length class	*N*	Depth	SD	*N*	Depth	SD
			Pink salmon			
≤350	12	109.6	12.5	2	86.0	17.0
351–380	94	113.9	15.0	15	90.5	9.3
381–410	276	123.0	14.2	81	91.9	9.8
411–440	361	135.6	16.1	80	97.8	9.0
441–470	295	152.5	17.2	5	95.8	9.2
>470	175	169.1	20.0	2	88.0	8.5
			Chum salmon			
≤500	19	129.7	11.2	9	110.6	15.2
501–525	61	142.9	11.9	31	119.4	9.2
526–550	89	152.4	13.9	63	127.3	11.0
551–575	155	162.2	14.0	124	134.0	12.7
576–600	241	175.6	15.3	112	142.3	13.5
601–625	248	186.5	15.9	98	151.3	14.8
626–650	140	195.4	17.7	28	163.5	15.1
>650	74	207.0	17.1	12	169.7	19.3

more variable for males than for females ($F = 2.55$, $P < 0.01$) (Table 2). It was also more variable than all ages of spawning male chum salmon ($F = 1.53$, $P < 0.01$). Male pink salmon are clearly not all equally sexually dimorphic in their body depth.

Body depths of female chum salmon, when they are considered as a homogeneous group, were more variable than for female pink salmon ($F = 1.29$, $P < 0.01$). However, when female chum salmon were compared with female pink salmon on an individual age basis, there was no significant difference in the degree of within-stock variance. Male chum salmon had greater variability in body depth than did females ($F = 1.29$, $P < 0.01$). Variability in body depth for 5-yr-old chum salmon was less than at younger ages, similar to the result in the analysis of postorbital–hypural length.

Sexual Dimorphism

The previous analysis has indicated that postorbital–hypural length and body depth varied between the sexes. To examine if the sex of all individuals in a population could be readily determined on the basis of body length and body depth only, we used both characters in discriminant analysis to classify the individuals. Body depth was the more important criteria in distinguishing the sexes. Most individuals' sex could be correctly identified (Table 7). Mean postorbital–hypural length of those male pink salmon that were misclassified as females when both characters were used in the discriminant analysis was significantly less than those correctly classified as males ($F = 11.34$; df = 1, 157; $P < 0.01$). There was no significant difference in length of pink salmon females that were classified correctly and incorrectly ($F = 2.72$; df = 1, 32; $P > 0.10$). Male chum salmon that were misclassified as females were again significantly smaller than males classified correctly ($F = 25.56$; df = 1, 658; $P < 0.01$). As with pink salmon, there was no significant difference in length for chum salmon females that were

TABLE 5. Mean body depth (mm), standard deviations, ranges, % difference in body depth between largest and smallest individual, and coefficient of variation (%) for odd-year pink salmon stocks.

Stock	Mean	SD	Range	(Max − min)/min (%)	CV
Males					
Glendale	116.7	14.8	94, 184	96	12.7
Quinsam	130.0	17.0	96, 188	96	13.1
Puntledge	111.0	6.1	103, 117	14	5.5
Skagit	145.7	22.3	101, 197	95	15.3
Snohomish	151.9	20.4	104, 188	81	13.4
Stillaguamish	157.1	22.5	115, 202	76	14.3
Phillips	145.0	21.5	105, 199	90	14.8
Keogh	116.2	11.5	92, 161	75	9.9
Adam	140.3	20.5	98, 190	94	14.6
Indian	136.5	21.2	98, 193	97	15.5
Kakweiken	127.4	25.4	84, 197	135	20.0
Wakeman	142.7	30.5	92, 214	133	21.4
Jones	138.5	17.5	102, 185	81	12.6
Coquihalla	136.6	18.3	104, 172	65	13.4
Fraser	143.0	18.9	99, 185	87	13.2
Vedder	156.4	20.2	105, 219	109	12.9
Harrison	159.2	24.8	101, 212	110	15.6
Thompson	137.0	17.1	103, 176	71	12.5
Seton	129.3	15.9	97, 178	84	12.3
Portage	130.8	15.5	106, 161	52	11.9
Females					
Phillips	93.1	10.9	71, 122	71	11.7
Keogh	102.1	6.4	88, 114	30	6.3
Jones	86.4	7.3	70, 102	46	8.5
Coquihalla	94.9	7.6	78, 114	46	8.0

TABLE 6. Mean body depth (mm), standard deviations, ranges, % difference in body depth between smallest and largest individual, and coefficient of variation (%) for chum salmon stocks in southern British Columbia.

	Male						Female					
Stock	*N*	Mean	SD	Range	(Max − min)/min (%)	CV	*N*	Mean	SD	Range	(Max − min)/min (%)	CV
Weaver	65	157.7	19.5	113, 203	80	12.4	35	130.6	11.9	105, 154	47	8.4
Vedder	106	185.0	19.8	138, 235	70	10.7	94	136.4	12.4	108, 167	55	9.1
Harrison	72	201.8	21.8	143, 235	64	10.8	64	136.7	14.8	103, 183	78	10.8
Squakum	10	169.6	25.5	137, 215	17	15.0	15	121.5	14.3	93, 147	58	11.8
Inch	39	157.1	12.7	131, 190	45	8.1	0					
Chehalis	49	173.3	18.7	132, 215	63	10.8	0					
Alouette	65	190.2	14.5	160, 225	41	7.6	0					
Chilqua	48	162.9	17.9	132, 212	61	11.0	0					
Nanaimo	17	185.4	20.6	152, 228	50	11.1	0					
L. Qualicum	109	165.3	22.0	109, 215	97	13.3	91	127.6	13.2	101, 160	58	10.3
B. Qualicum	128	170.5	22.3	118, 230	95	13.1	72	134.5	17.6	91, 184	102	13.1
Puntledge	88	186.7	21.6	141, 240	70	11.6	51	141.5	11.6	113, 175	55	8.2
Chemainus	24	172.7	23.8	131, 220	68	13.8	29	136.0	14.2	110, 170	55	10.4
Cheakamus	74	190.0	15.8	151, 225	49	8.3	26	140.9	14.8	118, 170	44	10.5
Squamish	27	178.9	16.9	152, 220	45	9.4	0					
Sliammon	106	151.7	16.8	120, 184	53	11.1	0					

classified correctly and incorrectly ($F = 0.82$; df = 1, 397; $P > 0.10$). Smaller males in both species tend to resemble females more closely than they do other males.

Discussion

Pink salmon are variable in size between the even- and odd-year broodlines, among stocks within a broodline, and between and within sexes within a stock. Godfrey (1959) indicated that pink salmon spawning in odd years in British Colombia were usually heavier and probably larger than those spawning in even years. Fraser River pink salmon were also reported to be larger than other odd-year stocks. Similar results were recorded in this study. Skud (1958) reported that weights

TABLE 7. Results of classification of individuals by discriminant analysis using postorbital–hypural length and body depth as the distinguishing criteria. Mean postorbital–hypural lengths (and standard deviations) of correct and incorrect classifications are listed for each stock.

Stock	Males				Females			
			Mean length				Mean length	
	N	% correct	Correct	Wrong	*N*	% correct	Correct	Wrong
Pink salmon								
Coquihalla	33	87.9	424.0 (26.8)	364.3 (28.3)	67	100.0		
Jones	64	96.9	425.6 (26.0)	382.0 (0.0)	36	100.0		
Keogh	66	83.3	392.7 (21.5)	387.0 (26.4)	34	94.1	397.3 (13.7)	381.0 (7.1)
Phillips	52	100.0			48	100.0		
Total	215	92.1			185	98.9		
Chum salmon								
Weaver	65	90.8	555.8 (42.0)	547.5 (34.6)	35	91.4	554.8 (31.8)	550.0 (26.0)
Vedder	106	95.3	598.2 (33.3)	574.2 (16.7)	94	98.9	576.0 (29.5)	560.9 (0.0)
Harrison	72	93.1	622.7 (33.3)	600.0 (16.7)	64	100.0		
Squakum	10	80.0	608.5 (37.4)	590.0 (20.1)	15	93.3	548.9 (29.5)	585.0 (0.0)
Chemainus	24	91.7	590.3 (31.7)	506.0 (37.4)	29	96.6	572.7 (34.3)	504.0 (0.0)
Cheakamus	74	89.2	628.9 (24.8)	580.0 (34.6)	26	92.3	595.4 (30.7)	610.0 (0.0)
L. Qualicum	109	93.6	590.9 (37.3)	545.5 (20.1)	91	95.6	578.9 (34.3)	568.0 (39.6)
B. Qualicum	128	94.5	599.1 (41.6)	582.8 (39.2)	72	93.1	684.6 (35.3)	585.0 (41.3)
Puntledge	88	90.9	596.9 (31.7)	564.5 (37.4)	51	98.0	573.9 (26.5)	550.0 (0.0)
Total	676	92.6			477	96.2		

of pink salmon in southeastern Alaska may vary from 1 to 5 kg, but this probably includes broodline, stock, and sex differences combined. Male pink salmon are larger than females, and males are more variable in length than females (Pritchard 1937). The largest males could be 50% longer than the smallest males, whereas the largest females could be 30% longer than the smallest females (Pritchard 1937). Similar results were again found in our study.

Dimorphism for secondary sexual characteristics is more pronounced in pink salmon than in any other *Oncorhynchus* species (Davidson 1935). Hump size or body depth is a striking example of a sexually dimorphic character that depends upon the state of sexual maturity, but other characters, such as fin size or scale number, not generally considered to be dependent upon the degree of maturity, are also sexually dimorphic (Berg 1979; Beacham et al. 1983). Males and females are usually readily identified on the basis of their morphology.

Male pink salmon are more variable in length and body depth than are male chum salmon. Although they differ in the degree of their variability, the chance of misclassifying a male as a female on the basis of its morphology was about equal in the two species. Smaller males were more likely to be mistaken for females than were larger ones. In a breeding system where males compete for access to spawning females, it may be advantageous for small males to resemble females in order to reduce aggression by larger males towards them, thus allowing them to remain near females. Pink salmon females may be accompanied by a number of males during spawning (Smirnov 1975; Chebanov 1980), and the smaller males act as "satellite" males. Schroder (1981) showed that smaller satellite males may fertilize a portion of the eggs of a spawning female chum salmon, as did Chebanov et al. (1983) for sockeye salmon females. Gross (1983) indicated that "jack" coho salmon males are able to obtain access to spawning females by avoiding aggressive encounters with dominant males, thereby maintaining a position relatively close to a potential spawning female, and sneaking in during spawning and attempting to fertilize some of the female's eggs. Similar observations have been reported for Atlantic salmon (*Salmo salar*) (Belding 1934) and for small male sunfish (*Lepomis*) Gross (1983). Female mimicry has been reported in several species of fish (Barlow 1967; Constantz 1975; Dominey 1980).

Female pink and chum salmon misclassified as males by discriminant analysis (based upon both body length and body depth) were the same length as those females correctly identified as female. Females maintain territories in breeding pink and chum salmon populations, and it would be of little or no advantage for females to mimic males. Morphological variance for sexually dimorphic traits should therefore tend to be less for female pink and chum salmon than for males. The results of our study, as well as those of Pritchard (1937), Berg (1979), and Beacham and Murray (1983), support that view.

Our study suggests some areas that should be explored further with regards to the high degree of variation in size of male pink salmon. Spawning pink salmon populations could be studied to determine if "satellite" males contribute significantly to fertilizing a female's eggs, as has been done with electrophoretic analysis for chum and sockeye salmon. Growth rates and survival of fry derived from eggs fertilized by males of different size could also be investigated.

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Responses of Sockeye Salmon (*Oncorhynchus nerka*) to Fertilization of British Columbia Coastal Lakes

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Addition of nitrogen and phosphorus fertilizer to several British Columbia coastal lakes has resulted in increased autotrophic and heterotrophic production and larger standing stocks of zooplankton. These changes at the primary and secondary trophic levels are reflected by increased in-lake growth of juvenile sockeye salmon (*Oncorhynchus nerka*) and larger outmigrant smolts. Evidence is presented that smolt size changes in fertilized lakes will lead to increases in the harvestable surplus of sockeye adults by promoting both increases in marine survival and an earlier age-at-return to the fishery.

L'apport d'azote et de phosphore dans plusieurs lacs côtiers de la Colombie-Britannique a entraîné une augmentation de la production autotrophe et hétérotrophe et des stocks actuels de zooplancton. Ces changements aux niveaux trophiques primaire et secondaire se sont traduits par une croissance accrue des saumons rouges (*Oncorhynchus nerka*) juvéniles en milieu lacustre et une plus grande taille des saumoneaux quittant le milieu. On présente des preuves que les variations de la taille des saumoneaux dans les lacs fertilisés amèneront des augmentations dans le surplus exploitable de saumons rouges adultes grâce à une plus grande survie en mer et à un retour précoce au sein du stock exploitable.

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Between the years 1969 and 1975, investigators with the Fisheries Research Board of Canada conducted an experimental study at Great Central Lake, British Columbia, to test the hypothesis that increasing the supply of inorganic nutrients during the growing season in an oligotrophic lake would increase production at succeeding trophic levels and would consequently serve as a useful technique to enhance the productivity of a stock of sockeye salmon (*Oncorhynchus nerka*). LeBrasseur et al. (1978) reported that during fertilized years, mean summer primary production increased fivefold, zooplankton standing stock increased 9 times, the percentage survival from estimated potential egg deposition to juvenile sockeye increased 2.6 times, while mean stock size of adult sockeye increased from <50 000 to >360 000. Given the apparent sevenfold increase in Great Central Lake adult sockeye returns compared with pretreatment "historic" levels, LeBrasseur et al. (1979) concluded that lake fertilization could serve as a highly cost-effective technique to enhance sockeye salmon. Thus, when the Salmonid Enhancement Program (SEP) was launched in 1977 as a joint effort of the Federal and Province of British Columbia Governments an expanded Lake Enrichment Program (LEP) was initiated by the Fisheries Research Branch (FRB) with funding provided by SEP.

Since 1977, LEP personnel have conducted an ongoing assessment of trophic responses to fertilizer additions and other environmental variations in as many as 17 lakes along the British Columbia coast (Fig. 1) (Stockner et al. 1980; Stockner 1981; Rankin et al. 1979; Perrin et al. 1984).

The purpose of this paper is twofold: first, we present results from selected lakes that demonstrate that nitrogen and phosphorus additions to a variety of sockeye nursery lakes have increased primary and secondary trophic level responses and that these changes have resulted in increased growth of underyearling sockeye in treated lakes; second, we provide evidence that suggests that larger smolts will experience improved survival at sea as well as decrease their age-at-return as adults.

Study Lakes Description

The coastal lakes of this study are spread over a wide geographic area (Fig. 1) and represent a variety of morphometric and hydrologic types. They share in common properties of extremely low phosphorus concentrations (1–3 μg TP$\cdot$L^{-1}), short water residence time (0.3–7.3 yr), and the extreme oligotrophic condition (avg. 1–4 μg TChl$\cdot$L^{-1}). The majority are warm-monomictic and range in mean depth from 13 to 212 m and in surface area from 1.8 to 51 km^2.

Faunistically the coastal lakes are characterized by low species diversity and low standing crops with respect to both zooplankton and fish communities. Midsummer zooplankton communities are generally dominated numerically by *Bosmina*

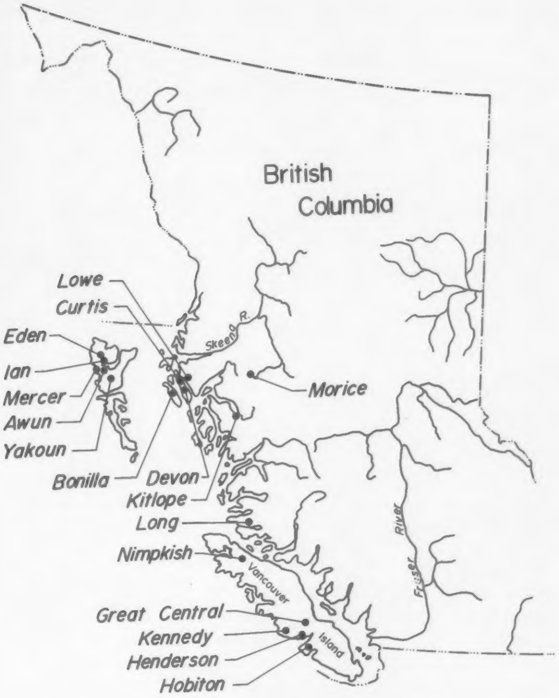

FIG. 1. Locations of treated lakes.

sp., and juvenile sockeye are the only fish consistently present in the offshore waters of all of the lakes. Threespine sticklebacks (*Gasterosteus aculeatus*) are the second most abundant fish in these lakes; however, they consistently occupy the limnetic zone during the summer growing season in only about one half of the study lakes. In the rest of the lakes, *G. aculeatus* appears to restrict its activities from April through September to littoral zone habitats. Due to the restricted area of littoral zone habitats in our coastal study lakes (generally <15% of a given lake's surface area, Table 1), the invertebrate and fish communities found there have not been systematically surveyed.

Methods

Water Chemistry and Primary Producers

Aqueous solutions of ammonium nitrate (NH_4NO_3) and ammonium phosphate ($(NH_4)_3PO_4$) were applied by air, using a DC6B aerial tanker, during the growing season (18–24 wk), and loads ranged from 2.5 to 14.8 mg $P \cdot m^{-2} \cdot wk^{-1}$ at atomic weight ratios of N:P ranging from 10:1 to 35:1 (Stephens and Stockner 1983). The limnological data reported here are restricted to the set of lakes from which samples could be taken at monthly or more frequent intervals to cover the period from near isothermal conditions in spring until the onset of fall overturn. Midlake sampling stations were established in the main basins of each lake. A 6-L Van Dorn bottle, rinsed with 95% ethanol, was used to collect all water samples obtained from 1-, 3-, 5-, and 30-m depths. Unfiltered samples were placed in a clean, rinsed test tube and a 125-mL rinsed glass bottle, stored in the dark at 4°C, and later analyzed for total phosphorus and total nitrogen. Samples for other nutrients and chlorophyll were stored for 2–4 h in 1- or 2-L polyethylene bottles and kept cold and in the dark. In the field laboratory, samples were ashed, washed, and filtered through 47-mm-diameter Whatman GFF filters and later analyzed for nitrate and total dissolved nitrogen. All samples were stored cold and in the dark, and chemical analyses were done at the Pacific Biological Station, Chemistry Laboratory, using the methods of Golterman (1969). A 500-mL sample was filtered under subdued light through a 47-mm-diameter, 0.8-μm Millipore filter, and a few drops of $MgCO_3$ suspension were added. Filters were folded in half, dried in a desiccator overnight, and then stored frozen and analyzed later for total chlorophyll using a Turner fluorometer (model 111) according to the method of Strickland and Parsons (1972). A test tube rinsed with 95% ethanol was rinsed and filled with sample water from 1, 3, 5, and 30 m for bacteria enumeration. In the field laboratory, 5 mL was filtered onto a 25-mm-diameter, 0.2-μm Nucleopore membrane filter counter-stained with Irgalan Black. Filters were air dried at room temperature (approximately 20°C) and stored. Samples were counted later under epifluorescence using the acridine orange direct count (AODC) method as described by MacIsaac et al. (1981).

Zooplankton

The general laboratory and field methods used by LeBrasseur and Kennedy (1972) in earlier studies of zooplankton were adopted as far as possible to maintain continuity with the present study. However, sampling frequencies differed since many of the lakes currently under study provide variable ease of access. Some of the large southern lakes (e.g. Great Central, Kennedy) are readily accessible by road and large boats, while the majority of lakes on the central and north coast are accessible only by float-equipped aeroplane. Thus, the frequency of zooplankton sampling by our program has varied from biweekly on the large southern lakes (Great Central, Henderson, Kennedy, Hobiton) in some field seasons (March–November) to one late season (July–September) sample only from many of the northern lakes. In this report, zooplankton biomass data from these late season samples are examined as a possible index of the outcome of fish-zooplankton interactions that have taken place across a given production season.

Samples for zooplankton biomass and species composition data were obtained from 25- to 50-m vertical hauls of a 0.25-m^2 black, cylinder-cone net with 100-μm mesh. Hauls were taken during the day at one mid-lake station per lake with the exception of Great Central, Long, and Ian lakes, which, due to their size, were sampled at two midlake stations. For the latter lakes, biomass data were expressed as the mean of the two samples. Where more than one late season sample was available for a given lake, we have arbitrarily used samples in order of priority from September, August, or July.

In the laboratory, net samples were halved with a Folsom plankton splitter. One half was filtered onto a preweighed, 0.45-μm Whatman glass fiber filter, dried at 90°C for 24 h, and weighed again. Biomass was expressed as milligrams dry weight per cubic metre. The other portion of the sample was used for enumeration and identification; however, only zooplankton biomass data are used in this report.

Sockeye Salmon

Addition of inorganic nutrients to lakes may potentially alter species interactions at each of several trophic levels in complex ways. However, in order for sockeye salmon to benefit, addition

TABLE 1. Summary of lake areas, hydroacoustic-and-trawl sampling effort, catches, and the proportion of limnetic fish communities composed of juvenile *O. nerka* in coastal study lakes during the 1980 field season.

Lake	Area (ha)	Area <5 m deep (%)	No. of transects	Total length of transects (m)	Fish·ha^{-1}	No. of trawls	No. of fish caught	% *O. nerka*	% age 1 smolts[a]
Devon	167	9.0	4	2 032	2796	5	2172	5.6	51.9
Long	1025	0.6	9	8 069	5658	14	1235	6.0	92.7
Kennedy Clayoquot	1480	3.2	7	9 790	2890	5	502	23.1	100.0
Kitlope	1058	12.1	4	3 978	129	5	34	29.4	67.0(1980)
Bonilla	207	10.1	4	1 838	2423	5	627	32.5	96.3
Henderson	1545	1.5	7	5 910	1811	5	48	43.7	100.0
Curtis	247	12.5	4	3 035	3224	5	1200	57.6	78.7
Nimpkish	3628	1.9	8	11 323	2572	5	148	89.9	100.0
Ian	1809	9.8	7	7 140	145	5	19	94.7	100.0
Great Central	5085	0.6	6	8 880	2400	9	620	96.8	96.6
Awun	465	5.4	4	2 521	839	5	445	97.1	95.9(1982)
Eden	556	8.8	4	3 502	374	5	83	97.6	96.0
Hobiton	350	4.6	5	2 170	870	5	57	100.0	99.4
Lowe	358	11.2	4	3 069	75	5	9	100.0	99.5

[a] Smolt samples obtained in the spring of 1981 with the exception of Kitlope and Awun lakes for which the closest sample years were 1980 and 1982, respectively.

of nutrients must alter trophic relationships such that juvenile sockeye either (1) experience higher within-lake survival or (2) attain larger size prior to seaward migration and then consequently experience higher marine survival. To be cost-effective, the sum of these marine and freshwater growth or survival effects must ultimately result in large enough increases in the biomass of returning adult sockeye that their dollar value to the commercial fishery more than offsets the costs associated with treatment, assessment, exploitation, and processing of a given stock. Therefore, our routine monitoring efforts have been focussed principally on sockeye for changes in freshwater growth, within-lake survival, marine survival, and total stock (i.e. catch and escapement). In a few instances, large magnitude changes in nontarget species have obviously altered sockeye production parameters in unexpected ways, and specific studies, which will be the subject of future reports, have been undertaken to explore the details of the response mechanisms involved.

Juvenile Sockeye Growth

Smolt size at the initiation of seaward migration serves as an index to detect differences in sockeye growth between treated and untreated years within the coastal study lakes. Since the spring of 1977, sockeye smolts have been sampled annually from 6–14 coastal lakes at varying intensity according to the scope of studies underway at a particular lake. Samples of up to 1274 yearling smolts have been obtained on as many as 20 dates within a single year from Great Central Lake. However, within a given calendar year the majority of lakes have been visited on two or three dates with the resultant acquisition of between 100 and 300 1-yr-old sockeye (Appendix). Samples were generally acquired between April 15 and May 15 by using large-mouthed (2 × 2 m) "drift" nets set in place at night, downstream of the outlet of a given lake. Although some samples of fish (Great Central, Henderson, Kennedy lakes) were returned immediately to the laboratory where fish weights and length measurements could be taken, the majority of fish were preserved in 10–25% formalin for a 5-wk interval, after which time blotted wet weight and fork length measurements were taken.

Preservation of fish in formalin tends to alter their weight and length measurements relative to fresh condition measurement (Parker 1963), and following recommendations of Parker, studies conducted in our laboratory indicate that smolts in our study are on average 10% heavier after 5 wk in formalin than their fresh weight counterparts. Consequently, mean weights of juvenile sockeye are reported here (Appendix) as formalin-standardized weights.

Partial age compositions of smolts in samples were determined from length frequencies and by examining either cellulose acetate impressions of scales or slide preparations of the actual scales. After examining the length-frequency distribution of fish in a sample, we prepared and read scales from fish that were large enough to possibly be older than age 1. Size comparisons of 2-yr-old smolts produced under treated and untreated conditions are not reported in this paper, since the number of observations and sample sizes for these fish are small. Two-year-old smolts were absent from 21 of 53 smolt samples obtained between 1977 and 1982 and constituted less than 10% of the fish in 40 of 53 samples (Appendix). Further, the lack of population estimates of fish in some years limits untreated observations of sizes achieved by 2-yr-old smolts, given known in-lake abundances over their two summers of lake residence, to only two observations between 1977 and 1982. Instead, we rely on the larger data sets pertaining to the mean sizes attained by 1-yr-old smolts to index differences in sockeye growth between treated and untreated years.

In-Lake Fish Population Estimates

Fish population estimates in the limnetic zone of each lake have been obtained through the application of hydroacoustic assessment techniques and complementary sampling with midwater trawl gear. Population census activities carried out by us between 1977 and 1982 relied on a Furuno, FM-21, 200-kHz sounder with 100 W of power output. On all surveys, we maintained the sounder at a constant pulse width of 1.0 ms and standardized gain settings at five steps above the lowest setting at which sockeye could be detected to accommodate a range of target strengths (see Thorne 1983). Our sounder was equipped with a time varied gain (TVG) circuit, which controls for spreading and attenuation losses of the acoustic signal with distance. The transducer was of the circular piston-type mounted on a hydroplane and was lashed into position alongside a 4-m-long inflatable boat. This positioning allowed depth strata greater than 2 m below the lake surface to be insonified. The effective beam width of the sounder was estimated to be 8° by measuring the relationship between the depth of a standard target (tournament quality ping-pong balls) and the distance from the acoustic axis at which a target, equivalent in strength to a juvenile sockeye, could be detected.

The number of cross-lake transects completed on a survey was based on lake size and basin complexity such that the total linear distance sounded on transects was roughly proportional to lake area (Table 1) and each basin of a lake was represented by at least one acoustic transect. Data from which population estimates could be made were restricted to the interval from midsummer to late winter due to seasonal changes in concentration in near surface waters which made juvenile sockeye unavailable to the sounder. Acoustic surveys were conducted at night and at intervals of several weeks to several months apart on a given lake. Nights for surveys were chosen whenever possible to provide light conditions that would be uniform throughout the sampling period. Adherence to specified transect lengths and locations both within and between trips was assured by marking the start and end points of transects with battery operated flashing lights at fixed shoreline locations.

Echograms from a survey were divided into up to as many as 12 depth strata with intervals increasing with depth for visual counting. Targets were counted in each stratum. Due to the narrow beam width, short pulse length, and relatively short range to targets on our surveys, target densities were only rarely high enough to produce a problem of coincidental counts for a stratum; consequently, unlike Barraclough and Robinson (1972), we have never had to resort to trawl catch data to establish the numbers of fish present within a given depth stratum. The volume of water sampled in a stratum varies due to both the conical shape of the acoustic beam (larger volumes are insonified at greater depths) and the variation in transect length at depth produced by bathymetric patterns unique to each transect. Therefore, raw counts have been adjusted to equivalent counts per unit volume. Means and 95% confidence intervals of abundance estimates are based on the adjusted counts for a given depth stratum from the four to nine acoustic transects completed for each lake. The estimate of mean abundance for a given lake and date is then simply the sum of the mean abundance estimates across all depth strata. To facilitate between-lake comparisons, abundance estimates are expressed as fish per hectare.

Data on the species and age composition of fish represented by targets are based on trawl catches. We used a midwater trawl that was 2 × 2 × 7.5 m in width, depth, and length, respectively. The trawl was constructed of a graded series of meshes from mouth (5.0-cm stretch mesh) to codend (1.3-cm knotless nylon). A 350-μm-mesh plankton net was attached to the codend of the net to reduce loss of scales in fish collected. Towing speeds were maintained at $1.0–1.5\,\mathrm{m \cdot s^{-1}}$. On each population survey, we completed a depth series of 5–14 trawls (Table 1) to establish species and age composition of fish over their main depth range as indicated by the echosounder. Because we have some concern over both the accuracy and precision of our species and age composition assignments based on unreplicated trawl catches within a given depth stratum, aggregate population estimates for all species and age groups in the limnetic zone are reported here; however, juvenile sockeye plus threespine sticklebacks always made up 95% or more of the catch from any lake. Other fish occasionally taken in small numbers were prespawning adult sockeye, juvenile coho (*Oncorhynchus kisutch*), peamouth chub (*Mylocheilus caurinus*), prickly sculpin (*Cottus asper*), and river lamprey (*Lampetra ayresi*). The combined catch of these other species never exceeded 5% of the total catch in any of our study lakes. Juvenile sockeye clearly dominated the catches from approximately half of our study lakes, while limnetic-dwelling sticklebacks were the most abundant species encountered in the other half (Table 1).

Adult Sockeye

Complications introduced by mixed stock fisheries, remote locations of spawning populations, and poor documentation of procedures used to generate historical escapement estimates (e.g. Pearse 1982) limit reliable data concerning total returns (catch and escapement) of adult sockeye to only 4 of the 13 lakes (Great Central, Henderson, Hobiton, and Long lakes) treated to date. Procedures used to obtain catch and escapement estimates for the above named stocks vary according to local circumstances but involve techniques and levels of effort such that large errors in estimates (>25%) are unlikely (Table 2). Fish scales and otoliths used to derive age structure and to assign returning adults to their appropriate brood years were sampled from catches and escapements.

Results and Discussion

In-Lake Response of Primary and Secondary Trophic Levels

For virtually every lake, phosphorus has been identified as the primary nutrient limiting phytoplankton production (Stockner et al. 1980; Stockner 1981). Owing to the extremely low ambient concentrations of total phosphorus in these coastal lakes (1–4 $\mu g \cdot L^{-1}$), phosphorus inputs from fertilizer during the growing season are far greater than natural inputs as shown by the good correlation between total phosphorus concentration (averaged over the growing season) and weekly phosphorus load from fertilizer (Fig. 2). Nitrogen, through the N:P ratio, plays an important role in determining the composition and size distribution of phytoplankton stimulated by nutrient additions (Schindler 1975; Tilman 1977), and consequently the suitability of phytoplankton as a food resource for herbivorous zooplankton (Gliwicz 1975). In all coastal lakes fertilized thus far, nutrient additions have increased both autotrophic (phytoplankton) and heterotrophic (bacteria) biomass (Fig. 3, 4). The greater abundance of bacteria and phytoplankton in all treated lakes has resulted in increased zooplankton production and biomass (LeBrasseur et al. 1978; Rankin et al. 1979) (Fig. 5).

Juvenile Sockeye Growth and Food Supplies

Evidence presented above and in other studies (Nelson and Edmondson 1955; LeBrasseur et al. 1978; Rogers 1979) supports the view that fertilization of the coastal lakes results in increased primary production and zooplankton abundance, which in turn should enhance the supplies of food that are available for young sockeye. A number of studies (see review in Brocksen et al. 1970) have shown that growth rates and sizes attained by sockeye within lakes are influenced by the quantity of zooplankton potentially available as food. However, this observation is by no means universal. LeBrasseur et al. (1978)

TABLE 2. Procedures used to estimate escapements and catches of adult sockeye to four coastal lakes receiving controlled nutrient additions.

Lake	Procedures used to obtain escapement estimates	Fishery type and procedures used to estimate catch
Great Central	Continuous electronic counts of adults through a fishway: 1975–82	Mixed stock fishery in Alberni Inlet. Catch estimated from sales slips. Catch allocated among three stocks (Great Central, Henderson, Sproat lakes) according to stock-specific patterns of parasite incidence in samples of fish taken from smolt runs and the commercial catch
Henderson	Multiple visual counts of adults on spawning grounds in Clemens Creek as well as mark–recapture population estimates; 1980–82	
Hobiton	Visual or continuous electronic counts of adults through a fence spanning the Hobiton River; 1980–82	Terminal, native-food fishery in Nitinat Lake only. Total catch estimates based on detailed monitoring of fishery by LEP contract personnel from 1980 to 1982
Long	Controlled, visual counts of adults through a fence spanning the Docee River; 1970–82	Single-stock, terminal fishery in Smith Inlet. Total catch estimated from sales slips

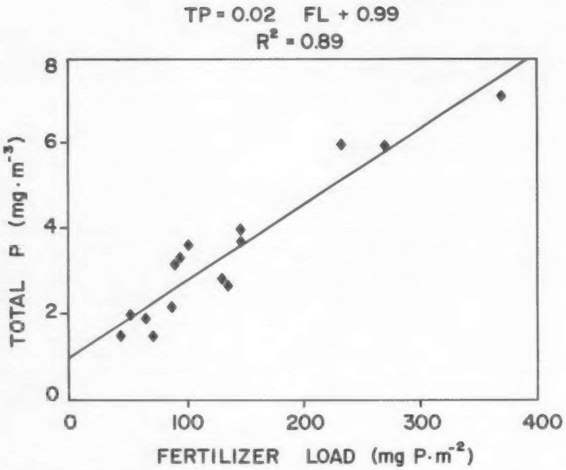

FIG. 2. Regression of seasonal average epilimnetic total phosphorus versus weekly phosphorus load added in fertilizer over the growing season for those lakes in 1980 and 1981 where seasonal averages could be computed ($n = 15$).

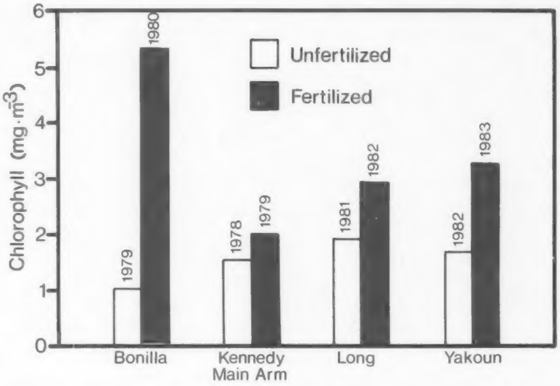

FIG. 3. Histograms comparing seasonal average total chlorophyll for four lakes for fertilized and unfertilized years.

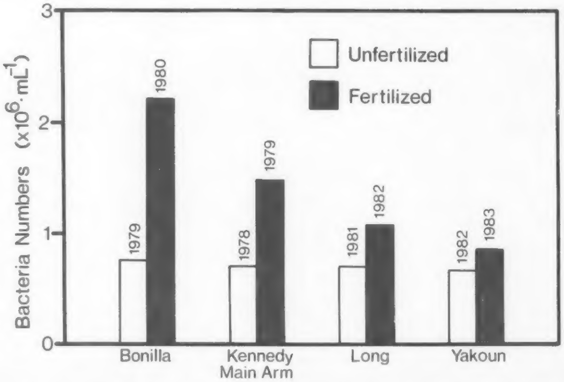

FIG. 4. Histograms comparing seasonal average bacteria numbers for four lakes for fertilized and unfertilized years.

found no significant correlation between zooplankton abundance and growth of sockeye to age 1 during 1969–76 when Great Central Lake was monitored under both treated and untreated conditions. By contrast, the weight of 2-yr-old smolts during treatment years was approximately twice that of 2-yr-olds in untreated years. Our data, from numerous coastal lakes, characterized by a wider range of limnological conditions (Stockner and Shortreed 1985) and fish densities than studied by LeBrasseur et al. (1978), leave little doubt that increases in the amount of zooplankton potentially available per fish have a significant ($p < 0.050$) influence on the weight that sockeye smolts achieve in 1 yr of growth (Fig. 6; equations 1 and 2 of Table 3). However, the simple regressions in Table 3 also clearly indicate that zooplankton biomass does not by itself account for the majority of the variation in sockeye smolt size among lakes and years ($r^2 = 0.22$) even when normalized to

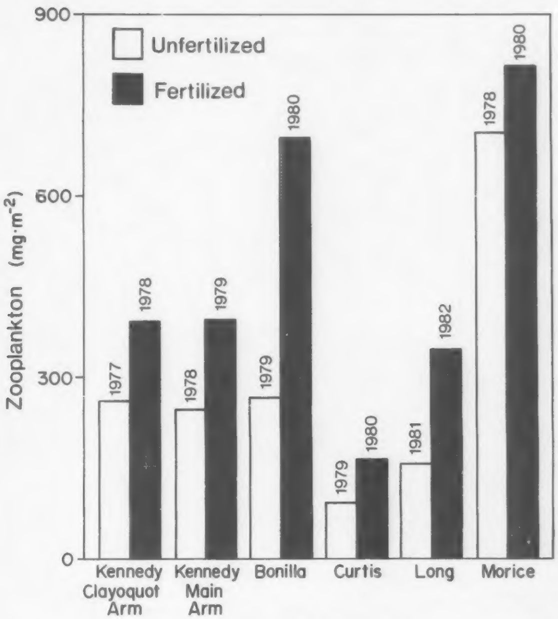

FIG. 5. Histograms comparing average seasonal biomass (measured dry weights) of zooplankton in six lakes during the initial year of treatment and the year immediately preceding treatment.

compensate for the abundance of fish drawing on zooplankton for food ($r^2 = 0.44$). Much of this residual variation is likely methodological, since, as pointed out by Hanson and Peters (1984), zooplankton biomass estimates, in particular, are likely to be inadequate where reliance is placed on a single vertical sample at a single sample site; this ignores the possibility of horizontal heterogeneity of zooplankton abundance. The opportunity to obtain more precise data was not available in the present study.

Smolt Sizes Attained under Treated and Untreated Conditions

Numerous studies on sockeye growth in lakes have revealed an inverse relationship between the abundance of fish (usually sockeye) per unit area of lake (density) and growth of young sockeye (Burgner 1962; Mathisen and Kerns 1964; Ruggles 1965; Johnson 1965; Rogers 1973; Goodlad et al. 1974). Consequently, comparisons of smolt size achieved in treated and untreated years or lakes must take into account between-year or between-lake differences in fish density. To do this we have pooled results for untreated or treated regimes for all lakes and years (Fig. 7). The pattern that emerges when considering smolt size variations under treated conditions suggests significant effects ($r^2 = 0.52$, $p < 0.001$) of fish density (predominantly sockeye and threespine sticklebacks) on sockeye growth. Fish density in treated lakes was the best univariate predictor of smolt size, surpassing even the multiple regression which included fish density and zooplankton biomass as independent variables (Table 3). Further, the data show a curvilinear relationship (Fig. 7a) in which small changes in fish numbers at low densities influence growth more than large changes in fish abundance at high densities (see also Rogers 1973). Under untreated conditions there is apparently no clear relationship between fish density and size attained by sockeye smolts (Fig. 7b); however, this is likely a consequence of the limited number of observations currently available rather than indicative that no such interaction exists. It is noteworthy that 12 of the 13 observations available for smolt sizes achieved in untreated lakes exhibit negative residuals to the relationship between fish abundance and smolt size in treated lakes (Fig. 7b). Comparison across the range of abundance for which both treated and untreated smolt observations are available indicates that on average smolts originating from treated lakes are 69% heavier than those from untreated lakes.

Significance of Changes in Smolt Size for Returns of Adult Sockeye

Background

A number of studies conducted over the past 20 yr indicate

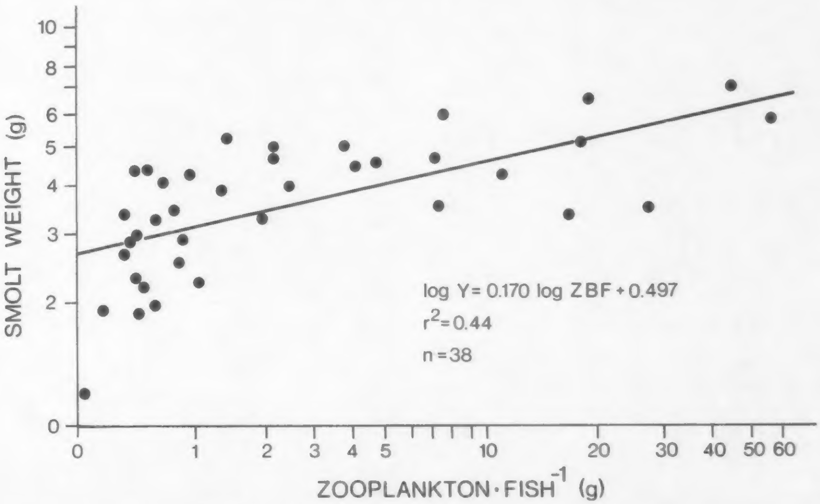

FIG. 6. Relation between the late season (July–Sept) biomass (g dry wt) of zooplankton maintained per fish in study lakes and the size (g wet wt) achieved by sockeye juveniles in their first year of lake residence. Lakes and years associated with particular data points are tabulated in the Appendix.

TABLE 3. Regression equations for predicting sockeye smolt size (Y in g wet wt) from zooplankton biomass (ZB in $mg \cdot m^{-3}$), zooplankton biomass per fish (ZBF in g dry $wt \cdot fish^{-1}$), fish abundance in untreated lakes (ZUF in $fish \cdot ha^{-1}$), fish abundance in treated lakes (ZTF in $fish \cdot ha^{-1}$), and fish abundance in all lakes (ZF in $fish \cdot ha^{-1}$).

	r^2	p^a	SE of slope	n
Simple regressions				
$\log Y = 0.231 \log ZB + 0.311$	0.22	0.003	0.072	38
$\log Y = 0.170 \log ZBF + 0.497$	0.44	<0.001	0.032	38
$\log Y = 0.002 \log ZUF + 0.347$	<0.01	0.986	0.107	13
$\log Y = -0.239 \log ZTF + 1.310$	0.52	<0.001	0.039	38
$\log Y = -0.227 \log ZF + 1.225$	0.32	<0.001	0.047	51
Multiple regression				
$\log Y = -0.238 \log ZF + 0.083 \log ZB + 1.204$	0.47	<0.001		38

[a] *F*-test.

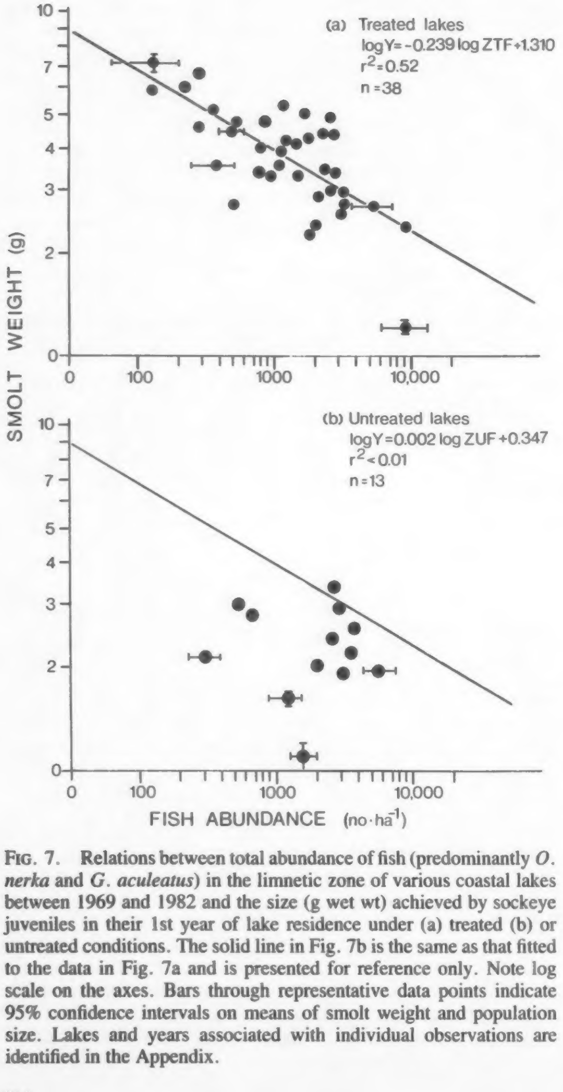

FIG. 7. Relations between total abundance of fish (predominantly *O. nerka* and *G. aculeatus*) in the limnetic zone of various coastal lakes between 1969 and 1982 and the size (g wet wt) achieved by sockeye juveniles in their 1st year of lake residence under (a) treated (b) or untreated conditions. The solid line in Fig. 7b is the same as that fitted to the data in Fig. 7a and is presented for reference only. Note log scale on the axes. Bars through representative data points indicate 95% confidence intervals on means of smolt weight and population size. Lakes and years associated with individual observations are identified in the Appendix.

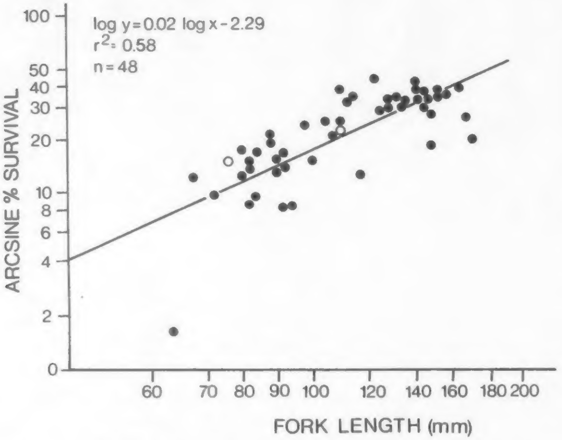

FIG. 8. Relation between smolt size (fork length) and variations in marine survival of sockeye reported by Ricker (1962, solid circles) and Peterman (1981, open circles). The solid line is the regression fitted to Ricker's data alone.

that natural or man-induced variations in smolt size may result in changes in the age composition, size composition, or "marine" survival of adult salmon to return for a given stock (Foerster 1968; Ricker 1962; Bilton 1971, 1978, 1980; Peterman 1981). Furthermore, the most recent of these have provided both empirical and analytical grounds to support the idea that smolt size does not achieve its influence alone but rather interacts with time of migration (e.g. Bilton et al. 1982) as well as smolt abundance at migration (Peterman 1981). Thus, the effect of smolt size variations on adult abundance and age-at-return for populations of sockeye are only likely to emerge from studies or analysis of natural populations which provide large numbers of observations that span a wide range of smolt size or from studies of intensively manipulated populations where the potentially confounding role of interacting variables may be controlled (e.g. Bilton et al. 1982). The data base we currently have on adult sockeye returns derived from treated brood years in the coastal study lakes satisfies neither of these conditions. Consequently, at this time, inferences concerning the effect on returning adult sockeye of larger smolts originating from fertilized coastal lakes must rely on the more extensive data sets

TABLE 4. Comparison of mean weights of yearling sockeye smolts produced in various lakes and regions. Mean weights (g) are summarized only for lakes and years during which the abundances of limnetic fish were estimated at between 1000 and 4000 fish$\cdot$ha^{-1}.

	Multilake, multiyear mean[a]	No. of lakes	Range of means across lakes and years[b]	Total observations
British Columbia,				
Untreated coastal[c]	2.12	9	1.0–3.4	16
Treated coastal[d]	3.57	10	2.0–5.2	25
Fraser and interior[e]	5.03	6	2.5–8.1	41
Alaska[f]	5.92	5	2.8–12.7	26
Washington State,				
Lake Washington[g]	12.20	1	11.7–12.7	3
USSR–Kamchatka,				
Lake Dalnee[h]	16.40	1	12.5–23.0	6

[a] Single values for each lake were used to calculate multilake means. If more than a single year of observation was available for a given lake, the mean of all years of observation was used to represent that lake's contribution to multilake means.

[b] All years of observation of mean smolt size were considered in defining the range of mean smolt size produced by a given group of lakes.

[c] Data from present study (Appendix) with the exception of three untreated years of observation at Great Central Lake by LeBrasseur et al. (1978) and four untreated observation years at Owikeno Lake by Ruggles (1965).

[d] Data from present study (Appendix).

[e] Data for Cultus, Chilko, Shuswap, and Fraser lakes are from Goodlad et al. (1974). Smolt weights for these lakes have been calculated on the basis of information in table 11 and fig. 5 of Goodlad et al. Relationships employed were as follows: (a) no. of freshwater circuli at Fraser Lake = 18.95–2.591 log female spawners$\cdot$ha^{-1}, Chilko Lake = 12.82–0.874 log female spawners$\cdot$ha^{-1}, Cultus Lake = 21.23–5.464 log female spawners$\cdot$ha^{-1}, and Shuswap Lake = 13.42–2.184 log female spawners$\cdot$ha^{-1}; (b) smolt weight (g) = 0.718 (circuli) − 5.03. Conversion from their use of female spawners$\cdot$ha^{-1} as an index of in-lake sockeye abundance to numbers of juvenile sockeye$\cdot$ha^{-1} are based on observations from 16 yr of counts at Cultus Lake and 20 yr of counts at Chilko Lake that the number of smolts produced$\cdot$female^{-1} has averaged 109 and 141, respectively. The mean of these values was applied for conversions at Shuswap and Fraser lakes where smolts have not been routinely enumerated. See Goodlad et al. (1974) for further details. Data for Babine–Nilkitkwa lakes are from Johnson (1961) and for additional years for Babine Lake from McDonald and Hume (1984).

[f] Data sources include Wood River Lakes system (Rogers 1979); Karluk Lake at which smolt sizes are from Barnaby (1944) and abundances after Rounsefell (1958); Larson Lake (Lebida 1984); Bear Lake (Kyle and Koenings 1983); Crescent Lake (Kyle 1983).

[g] Lake Washington data from Eggers et al. (1978).

[h] Lake Dalnee data from Krogius and Krokhin (1948).

that have been accumulated for stocks subjected to long-term assessment efforts.

Smolt size and marine survival

Ricker (1962) examined the effect of smolt size on marine survival by pooling data gathered over a 35-yr interval on six stocks of sockeye. These data suggest that on average increases in smolt size will result in substantial increases in survival to adults (Fig. 8). Using a somewhat different approach, Peterman (1982a) pooled extensive observations on body size and marine survival rates for sockeye, chum (*Oncorhynchus keta*), and coho salmon. He concluded that not only should larger smolts produce higher yields of adults, but they should also produce lower variability in adult returns for a given smolt abundance. It is noteworthy that the mean survivals at size calculated by Peterman for sockeye are of the same magnitude as those identified by Ricker (see Fig. 8). Given the general magnitude of smolt size increases achieved through fertilization of coastal lakes (Fig. 7), a twofold or greater average increase in marine survival of sockeye from treated lakes should occur.

However, populations of sockeye in coastal lakes currently under study produce smolts of the smallest mean sizes known for sockeye across their entire geographic range (Table 4), and limited data on smolt size and adult returns to coastal lakes (Table 5) indicate that marine survival variations between brood years are likely to be large. For example, the smallest smolts on which we have measured marine survival were derived from the 1977 brood year at Long Lake, yet in spite of their small size they have exhibited one of the highest marine survivals (30%) recorded by us to date. Indeed, multiple regression fails to reveal any strong effect of population size or smolt size on marine survival (survival = 22.83 − 0.71 abundance − 2.20 size, $r^2 = 0.16$, $N = 10$). This is not surprising given the small number of observations and the limited range of smolt sizes they cover (2.3–4.9 g; Table 5). Further assessment of marine survivals characterizing outer coast sockeye smolts of a wider range of sizes will be required to test whether treatment-induced changes in smolt size will on average increase marine survivals by the magnitude predicted from Ricker's data. In addition, further analysis is required to explain which features of our coastal

TABLE 5. Smolt sizes and marine survivals associated with specific brood years for four sockeye populations originating from coastal British Columbia lakes.

Lake and brood year	Presmolt population size (millions)	Mean weight[c] of smolts (g)	Survival to adults (%)
Great Central			
1975[a]	13.5	3.2	6.7
1976	7.8	4.5	7.2
1977	14.4	3.0	4.9
Long[b]			
1976	1.7	4.9	8.6
1977	2.5	2.3	30.0
Henderson			
1976	1.4	3.1	5.1
1977	1.1	4.1	8.8
Hobiton			
1976	0.35	3.9	6.1
1977	0.34	3.3	9.5
1978	0.19	4.7	29.2[d]

[a] Untreated brood year; juvenile sockeye from all other brood years experienced treated conditions.

[b] Preliminary estimates based on limited samples of scales to assign proportions of return to brood years.

[c] To enable ready comparison with data in Fig. 7, the range of smolt weights listed here corresponded to smolt fork lengths between 6 and 8 cm.

[d] Minimum estimate as data on 5-yr-olds that return in 1983 are not available yet.

study lakes (e.g. fast flushing rates, low zooplankton standing crops, nonoptimal thermal regimes) create conditions that are less favourable to good sockeye growth than are found for many sockeye nursery lakes in other geographic regions.

Smolt size and age-at-return

Reliable data to examine the influence of smolt size alone on age-at-return in sockeye are scarce. However, pioneering studies on sockeye (Krogius 1960, discussed in Foerster 1968) as well as hatchery experience with other species such as coho indicate that larger smolts will return as adults at a younger age (Hager and Noble 1976; Bilton 1971). In the case of coho populations, such advances in age-at-return result in production of a higher proportion of small 2-yr-old males ("jacks") (Hopley and Mathews, unpubl. manuscr., Salmon Culture Div., Wash. Dep. Fish.; Hager and Noble 1976; Bilton 1978) and a lower proportion of a single age-class (1.1) of returning adults. The situation is more complicated for sockeye where returns attributed to a given brood year may be associated with a large number of combinations of age-at-return (Table 6). What effect will increased smolt size have on age-at-return and therefore on biomass-at-return for "treated" coastal sockeye? Data sets for sockeye stocks associated with Owikeno Lake on the coast and Babine Lake in the interior may provide a partial answer. For both of these stocks, increases in smolt size of about the same magnitude as those experienced by smolts in treated coastal lakes result in an increase in the proportion of adults returning as

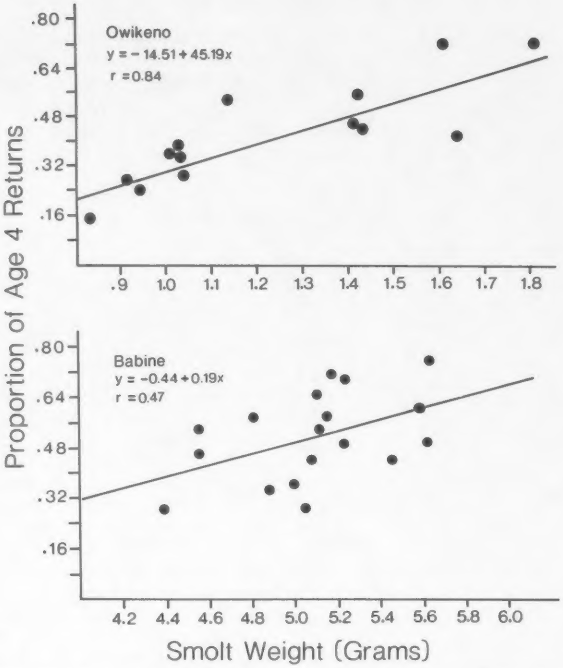

FIG. 9. Proportion of brood year adult returns migrating back at age 4 as a function of average smolt weight for that brood year for Owikeno Lake sockeye (D. Peacock, Department of Fisheries and Oceans, Prince Rupert, B.C., pers. comm.) and Babine Lake sockeye (from Peterman 1982a).

TABLE 6. Sockeye stock statistics and % age composition of escapements in 1981.

Lake	Sample size	% age composition[a]						Escapement	Total stock[b]
		1.1	1.2	1.3	2.2	2.3	Other		
Great Central	1337	8	65	22	3	2	—	262 000	853 000
Sproat	1181	13	65	18	2	<1	>1	127 500	419 000
Henderson	300	—	47	50	<1	<1	>2	35 000	75 000
Hobiton	493	2	61	36	1	—	—	17 000	25 000
Long	462	—	68	25	7	—	—	215 000	375 000
Bonilla	195	1	46	39	7	7	—	2 400	NA
Curtis	26	19	65	4	—	—	—	1 800	NA

[a] The European system is used to designate age. The first digit represents the number of winters sockeye juveniles spend in freshwater; the second digit represents the number of winters spent in the ocean.

[b] NA, total stock size cannot be reliably estimated due to interceptions of these fish in mixed stock fisheries off of southeast Alaska and northern British Columbia.

age 1.2 (Fig. 9) and an accompanying decrease in the proportion to return as age 1.3. Evidence that this trend may apply across a wide range of smolt sizes is available, as mean age of adult returns to the Naknek River in Alaska decreases in close association with increases in size (range 6–15 g) of both age 1 and age 2 smolts (Peterman 1982b). For sockeye, such advances in age-at-return are desirable with respect to maximizing the return of biomass of adult fish, as the size differences between age 1.2 and 1.3 or age 1.3 and 1.4 are not great enough to compensate for the mortality incurred through an additional year of ocean life. Also, to our knowledge, these shifts in age-at-return have not resulted in striking increases in the proportions of sockeye returning as "jacks" (i.e. age 1.1). Therefore, an acceleration of age-at-maturity through increased smolt size as a result of nursery lake enrichment will increase the harvestable biomass of sockeye.

Conclusions

The proportion of harvestable surplus obtained for a given stock and attributable to an increase in smolt size in treated lakes will have to be based on further refinement of our stock-specific knowledge of the complex interactions among population age structure, smolt size at migration, and effects of smolt size on marine survival and subsequent age-at-return of adult sockeye. Nevertheless, when interpreted within the general context of studies on factors affecting returns of adult sockeye, we are satisfied that our demonstration of a clear link between enhanced production at lower trophic levels and increased size of sockeye smolts migrating from treated lakes constitutes persuasive evidence to support predictions of significant gains in sockeye stock returns due to the application of lake fertilization as an enhancement technique.

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APPENDIX. Juvenile smolt samples from treated and untreated British Columbia coastal lakes.

Lake	In-lake year	Smolt weight (g)[c]	95% CI	*N*	Trips	Fish·ha^{-1}	Zooplankton·fish^{-1}(g)[d]	1+ smolts (%)
				Treated				
Great Central[a]	1970	2.90				2160		98.7
	1971	2.73				2160		77.6
	1972	4.20				520		96.4
	1973	2.70				3310		99.0
	1977	5.04	0.12	673	20	1700	3.78	74.8
	1978	3.36	0.04	1274	13	2880	0.31	94.7
	1979	5.26	0.10	406	7	1200	1.41	100.0
	1980	3.50	0.07	537	6	2400	0.78	96.8
	1981	4.27	0.13	190	3	2338	0.41	71.2
Henderson	1977	3.00	0.05	309	3	2600	0.40	100.0
	1978	4.12	0.08	442	3	1470	0.66	100.0
	1979	2.30	0.04	200	2	2000	1.05	100.0
	1980	2.25	0.06	264	3	1811	0.47	100.0
	1981	4.30	0.09	252	2	1802	0.94	100.0
Hobiton	1977	3.90	0.10	419	8	1150	1.33	100.0
	1978	3.31	0.10	185	4	975	1.92	100.0
	1979	4.70	0.17	323	3	540	7.08	99.4
	1980	4.77	0.15	169	3	870	2.13	100.0
	1981	3.34	0.12	229	2	1500	0.59	93.9
Kennedy	1978	2.55	0.09	147	2	3260	0.82	98.6
Long	1977	4.90	0.15	280	10	2640	2.18	85.4
	1978	2.33	0.06	242	3	9250	0.42	98.8
	1979	1.23	0.04	513	3	9160	0.05	100.0
Bonilla[b]	1980	1.96	0.09	211	2	2423		96.3
	1981	2.54	0.03	423	2	8524		98.6
Devon	1980	4.35	0.20	124	2	2796	0.51	51.9
Curtis	1980	2.93	0.10	266	2	3224	0.88	78.7
	1981	2.63	0.07	256	2	5350	0.31	85.9
Lowe	1979	3.56	0.08	207	3	1123	7.24	100.0
	1981	3.94	0.92	4	1	831	2.46	100.0
Kitlope	1979	4.57	0.37	63	2	287	4.79	67.0
	1980	5.83	1.24	4	1	129	56.00	100.0
Awun	1981	3.51	0.07	279	1	388	27.51	100.0
	1982	4.22	0.14	219	2	1238	11.09	93.6
	1980	5.97	0.25	84	1	225	32.60	100.0

APPENDIX (*Concluded*).

Lake	In-lake year	Smolt weight (g)[c]	95% CI	*N*	Trips	Fish·ha^{-1}	Zooplankton·fish^{-1}(g)[d]	1+ smolts (%)
Ian	1981	7.03	0.40	35	2	136	44.38	92.1
	1982	6.57	0.28	73	2	310	19.03	100.0
Eden	1980	5.14	0.18	97	1	374	18.05	100.0
	1981	4.45	0.18	57	2	503	4.17	48.3
	1982	3.41	0.09	232	2	705	16.77	93.2
Untreated								
Great Central[a]	1969	2.80				670		89.3
	1974	2.55				3760		91.0
	1975	3.00				520		56.5
Kennedy	1977	1.98	0.04	396	4	2025	0.59	100.0
Long	1980	1.96	0.04	408	3	5658	0.18	92.7
	1981	2.97	0.08	206	3	2969	0.38	98.1
Nimpkish	1980	2.40	0.17	30	1	2572	NS	100.0
	1981	2.75	0.06	355	4	3544	NS	100.0
Bonilla	1979	1.62	0.06	157	4	1222		95.7
Devon	1979	1.89	0.10	89	3	3102	0.44	84.0
	1981	3.35	0.10	111	2	2705		83.5
Curtis	1979	1.09	0.12	156	1	1589	1.09	100.0
Kitlope	1978	2.14	0.30	25	1	310	NS	100.0

[a] Data from Great Central Lake between 1969 and 1975 are from LeBrasseur et al. (1978); 95% CI, number of smolts collected and number of trips taken are not readily available (see LeBrasseur et al. 1978 for details). Late summer zooplankton values for Great Central Lake prior to 1977 have not been used, as LeBrasseur et al. (1978) did not routinely measure dry weights and there is uncertainty regarding the wet to dry weight conversion factor to use with their data (LeBrasseur and Kennedy 1972).

[b] Treated-year values for Bonilla Lake are excluded from analysis due to the presence of masses of *Chaoborus* sp. larvae which are detected by our acoustic gear and which "mask" the true abundance of fish.

[c] Smolt weights are blotted wet weights taken after 5 wk of preservation in 10–30% formalin. These weights are approximately 10% higher than fresh wet weights and 25% higher than wet weights taken after 5 wk in 70% ethanol.

[d] Zooplankton values are g dry wt·fish^{-1}. Zooplankton biomass samples are obtained from vertical net hauls carried out at midlake stations between July and late September (see Methods). NS = no sample.

Dispersion and Retention of Anadromous Rainbow Smelt (*Osmerus mordax*) Larvae in the Middle Estuary of the St. Lawrence River[1]

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Ouellet, P., and J. J. Dodson. 1985. Dispersion and retention of anadromous rainbow smelt (*Osmerus mordax*) larvae in the middle estuary of the St. Lawrence River. Can. J. Fish. Aquat. Sci. 42: 332–341.

The vertical and horizontal distribution of anadromous rainbow smelt (*Osmerus mordax*) larvae from hatching in their natal river to their occupation of nursery areas in the middle estuary of the St. Lawrence River was documented to describe the mechanism responsible for the retention of smelt larvae in this area. Peaks of larval abundance observed downstream of the spawning grounds indicate a 24-h periodicity in hatching and the introduction of larvae into the riverine circulation. No retention of larvae was observed between the spawning ground and the downstream portion of the natal river. Our evidence indicates daytime accumulation of larvae at the mouth of the natal river, possibly resulting from the negative phototaxis exhibited by small smelt larvae. Patches of smelt larvae were incorporated into the St. Lawrence estuarine water mass once every 24 h at night following high tide. The subsequent downstream transport of larvae in the St. Lawrence estuary appears slower than the advection of the water mass due to the tendency of larvae to remain deeper in the water column during ebb tides and to concentrate near the surface during flood tides. Smelt larvae are transported from the south shore to the partially mixed northern portion of the middle estuary which represents the principal zone of larval smelt accumulation. We propose that the vertical displacements exhibited by smelt larvae in combination with the two-layer circulation system of the northern middle estuary results in the retention of smelt larvae in this region.

La distribution verticale et horizontale des larves de l'éperlan anadrome (*Osmerus mordax*), de l'éclosion dans la rivière natale jusqu'à l'aire d'alevinage dans l'estuaire moyen du Saint-Laurent, a été étudié dans le but de décrire le mécanisme responsable de leur rétention dans l'estuaire moyen. L'échantillonnage effectué en aval des sites de frai a permis de révéler une périodicité de 24 h pour l'éclosion et la mise en circulation des larves. Aucune évidence de rétention larvaire a été noté entre les sites de frai et l'embouchure de la rivière. Pendant le jour, il y a accumulation des larves à l'embouchure de la rivière, possiblement due au phototactisme négatif observé chez les larves d'éperlan. En conséquence, des groupes de larves sont mélangés aux eaux estuariennes à toutes les 24 h, la nuit, suivant la marée haute dans la rivière. Dans l'estuaire les larves descendent vers le fond au baissant et remontent près de la surface au montant, ainsi le transport aval des larves est plus lent que l'advection net des masses d'eau. Les larves sont transportées de la partie sud vers la région nord de l'estuaire moyen du Saint-Laurent, qui est le site principal de l'accumulation des larves d'éperlan. Les déplacements verticaux exercés par les larves combinés à la circulation estuarienne en deux couches, dans le secteur nord de l'estuaire moyen, seraient le mécanisme responsable de la rétention des larves dans ce secteur.

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Three discrete geographical groups of anadromous rainbow smelt (*Osmerus mordax*) have been identified in Quebec waters (Fréchet et al. 1983) from (1) Baie des Chaleurs, (2) the south shore of the St. Lawrence River, and (3) the Saguenay fjord. Two major spawning sites were recognized for the St. Lawrence group (Fréchet et al. 1983; Magnin et Beaulieu 1965): (1) the Boyer River, located at the upstream end of the middle St. Lawrence estuary, and (2) the Ouelle River, located at the downstream limit of the middle estuary (Fig. 1). There are no spawning rivers reported from the north shore of the St. Lawrence middle estuary.

Fréchet et al. (1983) suggested that smelt do not home to natal rivers. However, they noted that the degree of heterogeneity in biological characteristics of spawning smelt of different geographical areas is less at the extremes of their Quebec distribution. They proposed the presence of isolating mechanisms that limit gene flow between geographical groups. Possibly, the discreteness of rainbow smelt groups is the result of larval retention occurring near the spawning rivers of each group.

Recent studies on the ichthyoplankton of the St. Lawrence river and estuary state that rainbow smelt larvae are restricted to the region around and upstream of Ile aux Coudres (Able 1978),

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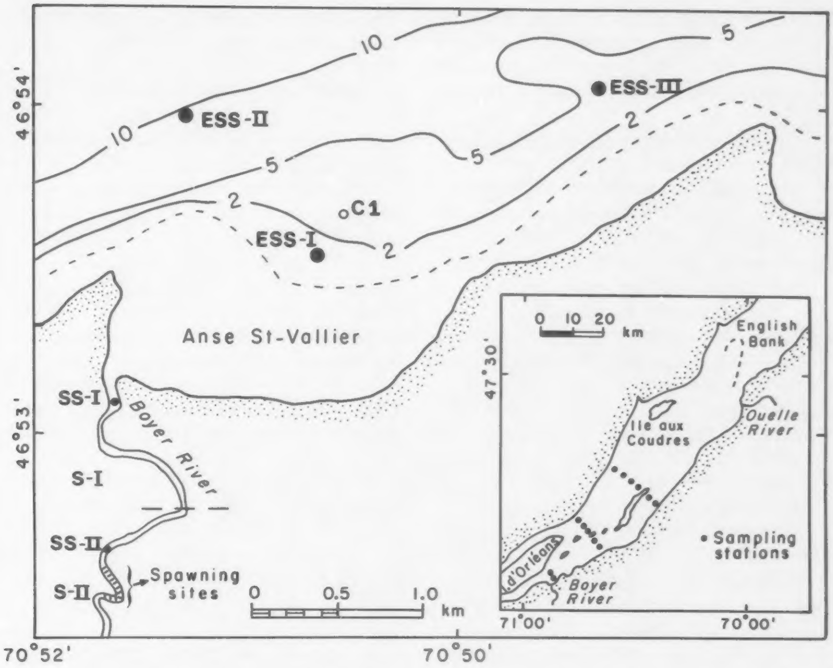

FIG. 1. Study area and location of sampling stations in the Boyer River and Anse St-Vallier. Inset illustrates the location of the three transects used for sampling the middle estuary. Isobaths are in metres. The broken line indicates low water level.

and Courtois et al. (1982) demonstrated that smelt larvae are isolated from other major species of the ichthyoplankton community, being associated with the fresher upstream water mass. Thus, smelt larvae are either retained in the northern upstream portion of the middle estuary or differential mortality (i.e. larvae that drift downstream, die, and disappear) occurs in this region. However, Able (1978) suggested that the larvae are capable of maintaining themselves in this zone by utilizing the upstream current near the bottom.

The mechanisms involved in larval fish retention in estuaries are already the subject of an extensive literature (see Fortier and Leggett 1982 for a review). Many of these models are developed for larval retention in partially mixed estuaries where the circulation pattern consists of a net seaward flow of the fresher (mixed) surface layer and a net upstream flow of salt water along the bottom (Dyer 1973). Hence, the mean vertical position of organisms in relation to the zone of net motion determines the magnitude and direction of larval transport. This mechanism implies active swimming behavior and possibly the capacity of larvae to remain in discrete layers of the water column.

Well-mixed estuaries have no vertical salinity gradient. Circulation is determined by tidal flow, and the mean flow is seaward throughout the water column (Dyer 1973). A model for larval retention in a well-mixed estuary was proposed by de Wolf (1973); he demonstrated that cypris larvae exhibit higher specific densities than the surrounding water and tend to sink to the bottom at slack water and are resuspended by the action of tidal currents. Thus, the larvae are trapped in estuaries in the same way as suspended matter. This mechanism does not require the existence of active larval swimming to explain the observed retention of cypris larvae.

The Boyer River is located on the south shore of the upper portion of the middle estuary and young smelt larvae emerging from this spawning site enter the estuary in a well-mixed region (Ouellet and Trump 1979). Thus, if there is larval retention in this area, it cannot be explained by the two-layer circulation that is characteristic of the northern middle estuary.

Our objectives were to document the dispersion of smelt larvae from the spawning ground of the Boyer River throughout the middle estuary and to investigate the factors contributing to their apparent retention in this zone. We hypothesized that passive mechanisms contributing to retention may act at any point during the early life history of smelt, from hatching and drift in the natal river, dispersal of larvae from the river's mouth, to the distribution of older larvae in the middle estuary and the development of active mechanisms of retention.

Materials and Methods

Study Area and Physical Assessment

Boyer River is a small tributary located on the south shore of the middle St. Lawrence estuary (Fig. 1). The river meanders through an agricultural region and opens into the estuary over Anse St-Vallier, a large tidal flat on the margin of the south channel. In 1982, work began on the river following spring break-up which coincides with the anadromous smelt run.

Six tidal gauges were positioned equidistant from the river's mouth to approximately 2 km upstream. The gauges were placed in the river bed a few metres from the bank. At each station, width and depth of the river were recorded. Along this section, 17 flow-measurement stations (FMS) were selected for direct measurement of the river flow using either a Marsh–McBirney (model 201) or Gurley portable water-current meter. Each FMS was chosen to be representative of the flow in a given portion of the river. Measures were taken in the main channel of each portion, midway in the water column.

An Aanderaa recording current meter was moored in Anse St-Vallier (C1, Fig. 1). The current meter was anchored such that the sensors were located midway in the water column at low water level. Unfortunately, suspended material damaged the speed sensor after only a few tidal cycles. Although there were no reliable current speed data available for the major part of the sampling program, a tidal speed curve was estimated based on speed data recorded at the beginning of the program.

The reliable speed curve was divided into five time intervals corresponding to periods of slack water, increasing speed, maximum speed, decreasing speed, and return to slack water. A numerical value was assigned to each time interval. Data recorded at the beginning of the program revealed that the highest speed values appeared during the flood. To represent this asymmetry, the coded tidal scale ranges from 0 to 4 for ebbing and from 0 to 5 for the flooding speeds.

There is a strong relationship between tidal amplitude and tidal current speed in estuaries (Dyer 1973). To keep this correspondance in our estimated tidal curve, we divided the tidal amplitude curve obtained at the beginning of the program into portions coinciding with the speed categories described above, and coded speed values were associated with the corresponding tidal stage. To standardize the partitioning of the tidal amplitude curve, we utilized the relation $0.5\ (1 + \cos m\pi)$ proposed by Legendre and Simard (1978). Tidal amplitude was rearranged on a unit scale ranging from 0 (high water) to 1 (low water). In the equation, m is defined as the difference between time of low slack water and the time limiting each speed category, divided by the time separating low and high slack water.

Sampling Stations and Procedures

Spawning sites were located by visual inspection of gravel and rocks picked up from the river bottom. Smelt eggs adhere to the substrate, and egg masses are easily identified.

Two stations, 1.5 km apart, were selected for sampling larvae drifting downstream: station I (SS-I) located at the river's mouth and station II (SS-II) located 100 m downstream of the spawning beds (Fig. 1). At each station a 0.5-m Standard conical plankton net equipped with a TSK flowmeter and fitted with a No. 6 (0.250 mm) mesh net was anchored in the main channel of the river. Water velocity at each station was sufficient to assure adequate filtering of the net during sampling. However, for high water conditions at SS-I, the net was towed horizontally midway in the water column using a 5.5-m inflatable Avon boat.

Three sampling stations were selected in Anse St-Vallier (Fig. 1). ESS-I and ESS-III are close to the south shore and at low water exhibit a depth of 2 and 4 m, respectively. ESS-II is located offshore toward the south channel and is the deepest station with a depth of 10 m at low water. Sampling at these stations was done using a 0.5-m Standard net equipped with a TSK or General Oceanic flowmeter and fitted with a No. 6 (0.250 mm) mesh net. For the shallow-water stations (ESS-I, ESS-III), sampling at high water consisted of step oblique tows from the bottom to the surface, whereas at low water a horizontal haul midway in the water column was conducted. The greater depth at ESS-II permitted the sampling of two discrete levels in the water column: a deep step-oblique tow from near the bottom to 3 m from the surface and a shallow horizontal tow 1 m under the surface.

Sampling stations in the middle estuary were located along three transects (Fig. 1). There was 20 km between adjacent transects, and 3–4 km separated stations along a transect. For the first of two surveys, only stations in the south channel were sampled. For the second survey, all stations of transects 2 and 3 were sampled. Sampling consisted of step-oblique tows from the bottom to the surface using a 0.5-m Standard plankton net equipped with a flowmeter and fitted with a No. 0 (0.500 mm) mesh net. For each survey, one station was chosen for hourly sampling over one tidal cycle during daytime hours. Despite the shallowness of the water column (6 m at S-4, first series; 7 m at S-12, second series; see Fig. 6) during ebb conditions, two discrete layers of the water column were sampled on these occasions: a horizontal surface tow and a horizontal tow close to the bottom.

Sampling in the Boyer River consisted of two 72-h series (May 17–20, 1982, and May 25–28, 1982) in which the upstream and downstream sections of the river (S-II and S-I, Fig. 1) were simultaneously sampled for smelt larvae (at SS-II and SS-I, Fig. 1) and for physical variables once every 3 h. Collection of a 10-min plankton net sample was followed immediately by the measurement of flow at each FMS and the recording of water level and temperature at each tide gauge station.

Sampling in Anse St-Vallier consisted of two 48-h series, each conducted immediately following a sampling series in the Boyer River (May 22–24 and May 30–31). The second series was suspended after 36 h because of severe weather. Successive samples at ESS-I, ESS-II, and ESS-III (Fig. 1) were repeated every 3 h. Collection of a 10-min plankton net tow was immediately followed by the recording of temperature and salinity profiles.

Sampling in the middle estuary was conducted on June 8 and 12, 1982. On both occasions, sampling began at high slack water at transect 3 and progressed upstream. Temperature and salinity were recorded at each station following the plankton net sample. Tidal stage at each station was estimated according to the relation $0.5\ (1 + \cos m\pi)$ (Legendre and Simard 1978), where times of low and high water were obtained from Canadian Hydrographic Service tide tables. Sampling over one complete tidal cycle consisted of hourly plankton net samples and current, temperature, and salinity profiles over a period of 13 h, conducted on June 9 and 13, 1982.

Sample Treatment and Analysis

All samples were preserved in 4% formalin. Samples containing less than 200 smelt larvae were completely sorted. Samples containing more than 200 larvae were subsampled using a Folsom partitioner. Fifty smelt larvae were randomly chosen from each sample and measured to the nearest 0.05 mm. Numbers of smelt larvae were standardized for a unit volume of water filtered ($100\ m^3$).

We tested for differences in length–frequency distributions of larvae collected at different sites and at different times with the Kolmogorov–Smirnov two-sample, one-tailed test (Siegel 1956). For the riverine series, larvae sampled at high water at the river's mouth (SS-I) were excluded from the analyses in order to compare only smelt larvae issued from the spawning ground (SS-II) and still present at the river mouth station during the ebbing phase of the tidal cycle.

A contingency table analysis (Legendre and Legendre 1979) was performed on the data obtained for the series at ESS-II to determine the contribution of light conditions and tidal phase to the conditional probability distribution of the abundance of smelt larvae at different depths. It is possible to test a posteriori if an observed value (O) in the table significantly differs from the associated expected value (E). A test value is calculated with the expression

$$\frac{|O - E|}{\sqrt{O(1 - O/p)}}$$

where p represents the total number of observations in the contingency table. If the result obtained is greater than the value $(1 - 2\alpha/rc)$, where $\alpha = 0.05$ and represents the probability level of significance, r represents the number of rows, and c represents the number of columns in the contingency table, we concluded that the observed value is significantly greater than the expected value.

Results

Hydrology

A single spawning ground was located 2 km upstream from the river's mouth (Fig. 1), in an area of high flow velocities (mean = 0.85 ± 0.23 m/s), at a mean depth of 33 cm. During the first sampling series this area was above the upstream limit of tidal incursion.

A pool characterized by increased depth and low water velocity located 1 km downstream of the spawning ground divides the river into two sections. The first region (S-I, Fig. 1), from the mouth of the river to the pool, is characterized by low flow velocity (mean = 0.18 m/s) and is of variable depth and width (mean depth = 50.0 ± 27.3 cm; mean width = 24.9 ± 7.3 m). The second portion (S-II, Fig. 1), from the pool to the spawning site, is characterized by higher flow velocity (mean = 0.49 m/s) and relatively uniform depth and width (mean depth = 31.9 ± 11.1 cm; mean width = 18.5 ± 3.6 m).

S-I represents the estuarine portion of the Boyer River. Tidal amplitude at the river's mouth was 1.37 ± 0.36 m at neap tides and 2.34 ± 0.08 m for spring tides. On neap tides, more than 90% of the intertidal water volume is included in S-I, whereas on spring tides this section contains less than 70% of the intertidal water volume. Hence, fluctuations in water level and flow conditions in S-II occur during spring tides in the estuary.

The tidal curve for this region of the estuary is asymmetric, showing longer ebbs than floods (ebbs, mean = 6.8 ± 0.5 h; floods, mean = 5.4 ± 0.1 h) with highest tidal speed occurring during flood (Fig. 2a). These features influence the tidal curve recorded in the river (Fig. 2b). The flood enters the river's mouth only when maximum water levels are attained in Anse St-Vallier. However, as this is associated with declining flood tide speeds in Anse St-Vallier, ebb tide conditions are quickly reestablished in the river. Thus, the ebb condition in S-I (Fig. 1) is much longer than the flood condition and the estuarine water mass penetrates the river only during a period of 2–3 h per tidal cycle (Fig. 2b). The net seaward residual flow was 0.21 ± 0.05 and 0.18 ± 0.06 m/s for the two sampling series.

The mean freshwater discharge during the first sampling series was 1.83 ± 0.44 m^3/s declining to 1.24 ± 0.49 m^3/s for the second series. These values represent normal flow conditions following spring runoff.

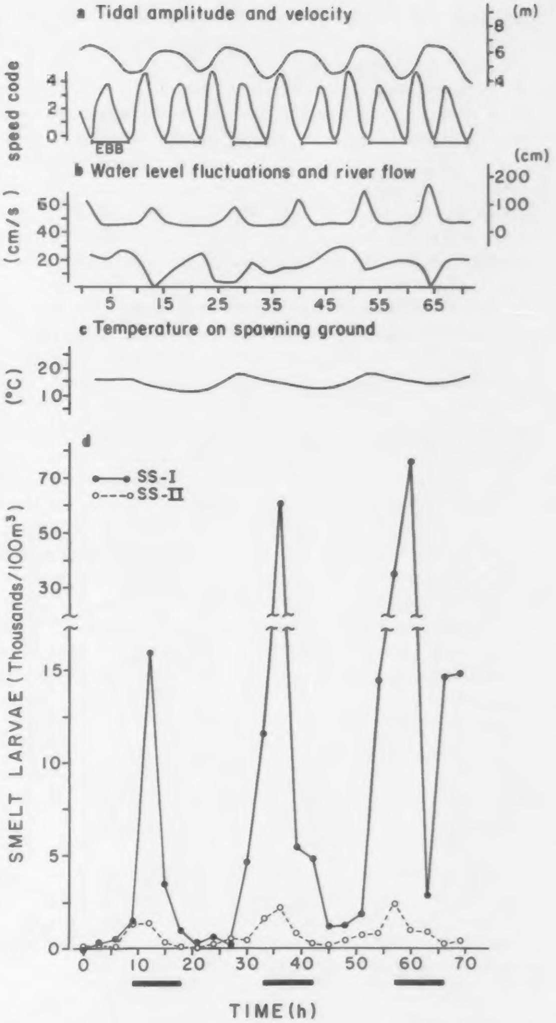

FIG. 2. Results of the first 72-h sampling series in the Boyer River on May 17– 20, 1982. (a) Tidal amplitude and speed (coded values) at Anse St-Vallier; (b) water level fluctuations and river flow at SS-I; (c) water temperature fluctuations on the spawning grounds; (d) larval densities at SS-I and SS-II; horizontal black bars indicate hours of darkness.

Hatching and Larval Drift in the River

Adult smelt were first observed in the river on May 4 and eggs were found on the river bed 2 d later. Smelt larvae were initially caught on May 16, for an estimated incubation time of 10 d at a mean water temperature of 9°C. Both sampling series covered the entire period of hatching, but the first 72-h series includes the initial peaks of hatching (Fig. 2d), permitting the sampling of the greatest number of larvae. The second sampling series conducted 5 d later initially revealed low densities of smelt larvae (500/100 m^3) declining to approximately 50/100 m^3 at the end of the 72-h period. Thus, the riverine drift of smelt larvae appeared almost completed by May 28.

The first sampling series revealed a 24-h periodicity in larval abundance correlated to water temperatures measured on the spawning grounds (Fig. 2c, 2d). A cross-correlation function revealed that peaks in larval abundance were out of phase with temperature peaks by 6 h ($P < 0.05$), maximum temperatures appearing at the end of the day, and peaks in larval abundance occurring at night. There was no significant correlation between river flow and larval densities at either the upstream or downstream stations ($P > 0.1$).

Larval densities measured at the downstream (SS-I) and upstream (SS-II) stations were significantly correlated (Kendall's tau = 0.705, $P < 0.001$, first series), with peaks of larval abundance at SS-II preceeding the peaks at SS-I by a maximum of 3 h (Fig. 2d). Larval densities observed at the river's mouth were much higher and more variable than those observed upstream (mean density at SS-I = 11 386.2 ± 19 486 larvae/100 m^3, C.V. = 171%; mean densities at SS-II = 697.6 ± 672.1 larvae/100 m^3, C.V. = 97%). Differences in larval abundance between the upstream and downstream stations increased within a single tidal cycle and throughout the 72-h sampling period (Fig. 2d). The increase in densities of larvae at SS-I occurring every two tidal cycles was followed by a sudden decline associated with the brief high tide and ensuing ebb at the river's mouth. A similar analysis of trends in larval abundance observed during the second 72-h series was not carried out due to the very low densities of smelt larvae present in the river.

Smelt larvae captured during riverine conditions (high-water samples excluded) at the river's mouth (SS-I) were slightly larger than those captured upstream (SS-II) during both 72-h sampling series (Fig. 3a, 3b) (Kolmogorov–Smirnov test: first series, $D_{\max} = 0.21$, $P < 0.001$; second series, $D_{\max} = 0.18$, $P < 0.001$). Smelt larvae captured during the first series exhibited a unimodal length–frequency distribution with the largest larvae and the greatest range of lengths observed at high water (Fig. 3c). During the second series, larvae captured at high water exhibited a wider range of lengths and a second mode appeared at 11.5 mm (Fig. 3).

Dispersion from the River's Mouth

The first 48-h sampling series conducted in Anse St-Vallier following maximum larval densities observed in the river revealed that smelt larvae were more abundant at stations farther offshore (ESS-II, mean = 1620.9 ± 991.6 larvae/100 m^3) and downstream (ESS-III, mean = 1945.4 ± 2055.4 larvae/100 m^3) than in the vicinity of the river's mouth (ESS-I, mean = 946.1 ± 867.1 larvae/100 m^3). Peaks of larval abundance at each station were associated with high-water conditions (Fig. 4). Differences in larval abundance between stations and the periodicity of peaks in larval abundance over the tidal cycle were not evident during the second sampling series due to the low numbers of larvae captured (ESS-I, mean = 207.9 ± 193.1 larvae/100 m^3; ESS-II, mean = 158.7 ± 85.3 larvae/100 m^3; ESS-III, mean = 176.8 ± 106.4 larvae/100 m^3.

The vertical position of smelt larvae in the water column, studied at station ESS-II, was dependent on light conditions (contingency table analysis, first series, $\chi^2 = 1018.5$, $P < 0.001$; second series, $\chi^2 = 31.8$, $P < 0.001$) and tidal currents (contingency table analysis, day samples, $\chi^2 = 23.54$, $P < 0.001$; night samples, $\chi^2 = 1013.8$, $P < 0.001$, for the first series). For both 48-h series, larvae were more abundant than would be expected by chance near the surface at night and in the deeper portion of the water column (>3 m) during daylight ($P < 0.05$). To evaluate the effect of the interaction between tides and light, we analysed the vertical position of larvae during flood and ebb conditions for daylight and night samples. During the night, smelt larvae were more abundant than would be expected by chance at the surface on flood tides ($P < 0.05$) and more abundant in the deep stratum (>3 m) on ebb tides ($P < 0.05$). However, during the day, the observed negative phototaxis of larvae appears to partially inhibit the vertical movement of larvae during flood tides. Although larvae were still more abundant than expected at the surface on flood tides ($P < 0.05$), larvae were as abundant as expected in deeper water ($P > 0.05$).

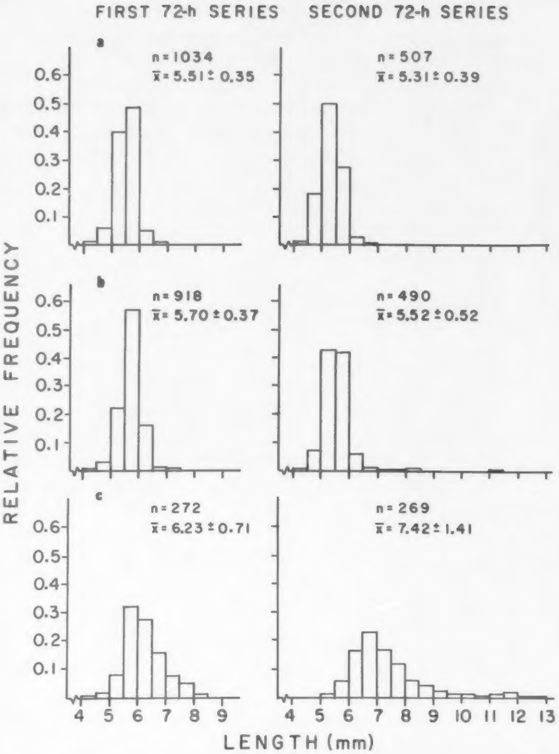

FIG. 3. Length–frequency distributions of smelt larvae sampled in the Boyer River on May 17–20, 1982 (first series), and on May 25–28, 1982 (second series); n = number measured, $\bar{X}$ = mean ± SD. (a) Larvae sampled at SS-II; (b) larvae sampled at SS-I (high-water samples excluded); (c) larvae sampled at SS-I during high-water conditions.

Length–frequency distributions of larvae sampled during the first 48-h series were unimodal (Fig. 5), but significant differences in length existed between stations. Larvae sampled offshore (ESS-II surface and bottom tows) were significantly smaller than larvae sampled at ESS-I ($D_{\max} = 0.424$, $P < 0.001$) and at ESS-III ($D_{\max} = 0.297$, $P < 0.001$). During the second series, larvae sampled offshore (ESS-II, surface and bottom tows) were again observed to be significantly smaller than larvae sampled at ESS-I ($D_{\max} = 0.362$, $P < 0.001$) and ESS-III ($D_{\max} = 0.284$, $P < 0.001$). The length–frequency distribution of these larvae at all stations revealed greater ranges

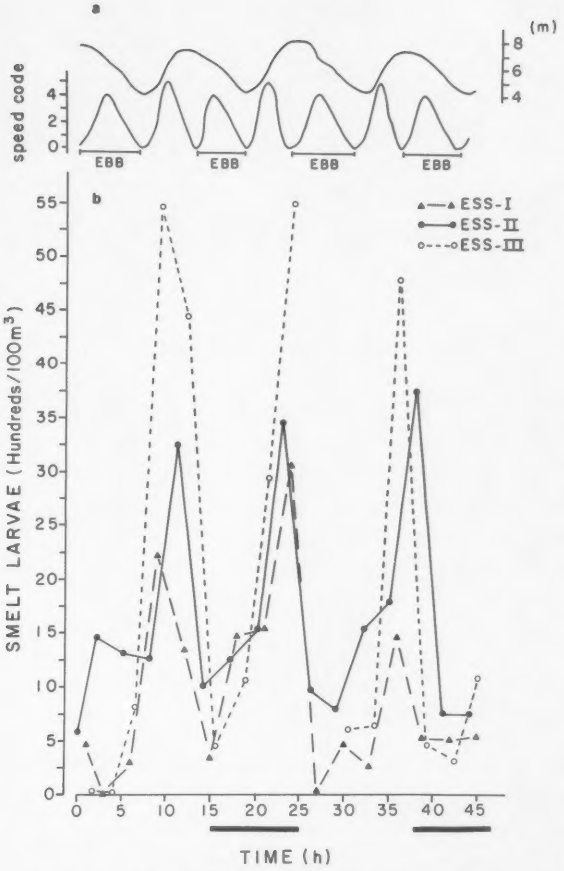

FIG. 4. Results of first 48-h sampling series in Anse St-Vallier on May 22–24, 1982. (a) Tidal amplitude and speed (coded values) in Anse St-Vallier; (b) larval densities sampled at ESS-I, ESS-II, and ESS-III; horizontal black bars indicate hours of darkness.

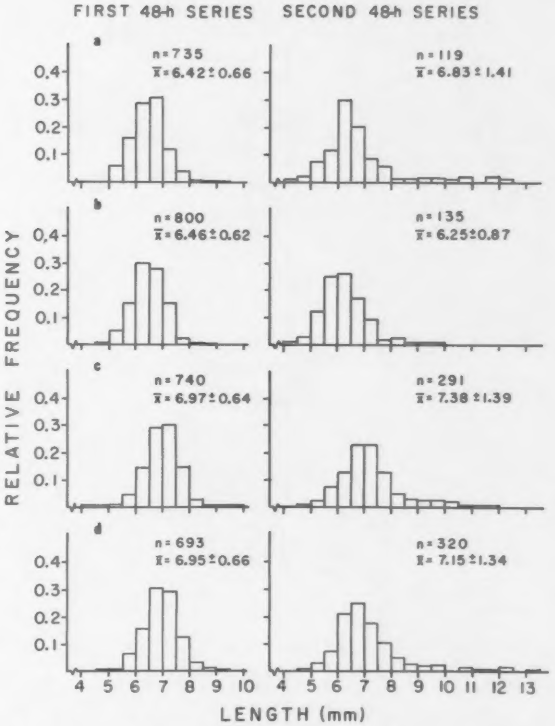

FIG. 5. Length–frequency distributions of smelt larvae sampled in Anse St-Vallier on May 22–24, 1982 (first series), and on May 30–31, 1982 (second series); n = number measured, $\bar{X}$ = mean ± SD. (a) Larvae sampled in surface tows at ESS-II; (b) larvae sampled in bottom tows at ESS-II; (c) larvae sampled at ESS-I; (d) larvae sampled at ESS-III.

and larger larvae with a second length mode appearing at the downstream and offshore (surface tows) stations (ESS-III, ESS-II, Fig. 5).

No significant differences in length were observed between larvae sampled in bottom and surface tows during the first 48-h series at station ESS-II (Fig. 5). During the second series, however, smelt larvae caught near the surface were larger than these caught near the bottom (Fig. 5a, 5b) ($D_{\max} = 0.19$, $P < 0.05$).

Distribution in the Middle Estuary

The two sampling series conducted in the middle estuary revealed a lateral gradient in the densities of smelt larvae, with the greatest densities occurring in the middle and northern section of the estuary (Fig. 6). No smelt larvae were captured on transect 1 in the vicinity of the Boyer River on June 8, and larvae were observed to be rarer in the south channel on June 12 than on June 8. Length–frequency distribution of larvae caught at all stations revealed a great range of lengths with many modes (Fig. 7, 8).

The vertical position of smelt larvae in the middle estuary was documented at S-4 (transect 2, Fig. 6) on June 9 and at S-12 (transect 3, Fig. 6) on June 13. On both occasions, the density of larvae caught in surface tows increased during the flood tides, while during ebb tides, larvae were more abundant in bottom tows (Fig. 9).

Discussion

Dispersion of Smelt Larvae

The 24-h periodicity in larval abundance peaks observed downstream of the spawning ground (SS-II, Fig. 1) at night appears to be the result of discrete hatching events associated with maximum water temperatures occurring at the end of the day. Although water temperature is a well-documented determinant of hatching in fishes (Braum 1978; Blaxter 1969), we are unable to explain the apparent 6-h lag between maximum temperatures and maximum larval densities. Thus, the relation observed is possibly an artefact of the relation between water temperature and the diurnal cycle. Nevertheless, as larval density was not correlated with water flow and as daytime net avoidance by newly hatched larvae is improbable, we concluded that the observed peaks in larval abundance represent a 24-h periodicity in the introduction of larvae into the riverine circulation. The 3-h time interval separating the occurrence of larval density maxima at SS-II and SS-I probably represents the time taken by larvae to reach the river's mouth, the transport time for a neutrally buoyant particle to drift passively from the

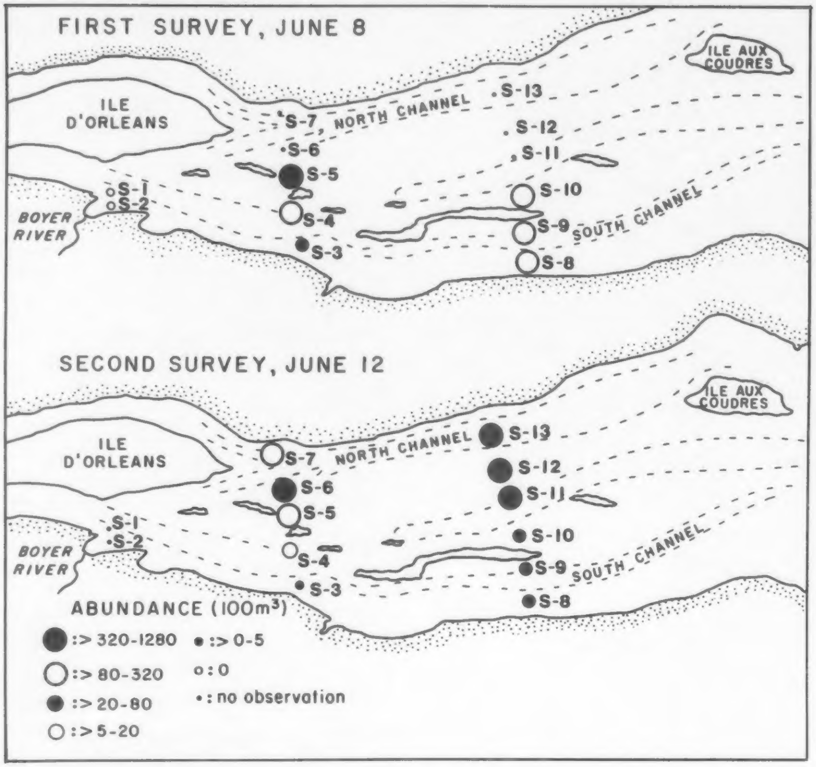

FIG. 6. Distribution and abundance (larvae/100 m^3) of smelt larvae sampled in the St. Lawrence middle estuary on June 8, 1982 (first survey), and on June 12, 1982 (second survey).

spawning grounds to the river's mouth, estimated using river flow data, being 3–4 h. Thus, from our observations we suggest that no larval retention occurs between the spawning grounds and the downstream portion of the river.

The increase in magnitude of successive peaks of maximum larval densities observed over 72 h at the river's mouth (Fig. 2d) is proportionately greater than the increase in magnitude of peaks in hatching observed downstream of the spawning ground. Although the majority of these larvae appear to be flushed from the river at night, following high tide, there is also a successive accumulation of larvae observed at the river's mouth during the day. These larvae are not flushed from the river following high tide during the day. Thus, the increase in magnitude of abundance peaks observed at SS-I appears to be due to two phenomena: night-time peaks in hatching and the accumulation of larvae drifting during the day from SS-II.

Sampling in the main channel of the river may have biased larval abundance estimates at SS-I. Smelt larvae emerging from the spawning grounds (S-II, Fig. 1) may be increasingly concentrated within the main channel of the river as they passively drift downstream. Thus, sampling at the main channel at SS-I may overestimate larval densities for the downstream section of the river. Nevertheless, daytime accumulation of larvae is supported by the observation that larvae sampled at the river's mouth (SS-I) during ebbing conditions are larger than larvae sampled at SS-II. The difference in mean length of approximately 0.2 mm which, when compared with the average growth of smelt larvae in this region (0.15 mm/d, Fortier and Leggett 1982; 0.24 mm/d, Able 1978), gives a period of growth in the river of approximately 24 h. We therefore propose that larvae remain in the river for an average of two tidal cycles before being flushed, thus explaining the progressive accumulation of larvae at the river's mouth observed over the 72-h period. As a result of this drift pattern, patches of smelt larvae are incorporated into the estuarine water mass following high tide every 24 h.

The appearance of large larvae in the samples taken in the river's mouth during high tide (Fig. 3) and the presence of large larvae in Anse St-Vallier indicate that smelt larvae remain in the proximity of the river once flushed from the river. Larvae sampled during the first 48-h series exhibit a unimodal length–frequency distribution at all stations, and their mean length indicates a period of growth of 5–6 d after hatching. Although differences in abundance between the three stations in Anse St-Vallier indicate a transport of larvae offshore and downstream, we conclude that the transport of larvae out of Anse St-Vallier is slower than the net downstream advection of the estuarine water mass, estimated at 1.4 km/d. The second 48-h series conducted 6 d later revealed low concentrations of larvae resulting from the declining hatching of smelt larvae in the river as well as the net downstream transport of older larvae. However, the length–frequency distribution of larvae sampled during the second 48-h series indicates the mixing of two groups of larvae (Fig. 5): a group of young larvae recently emerged from the river and a second group of older, larger larvae believed to correspond to the first larvae to leave the river. Smelt larvae

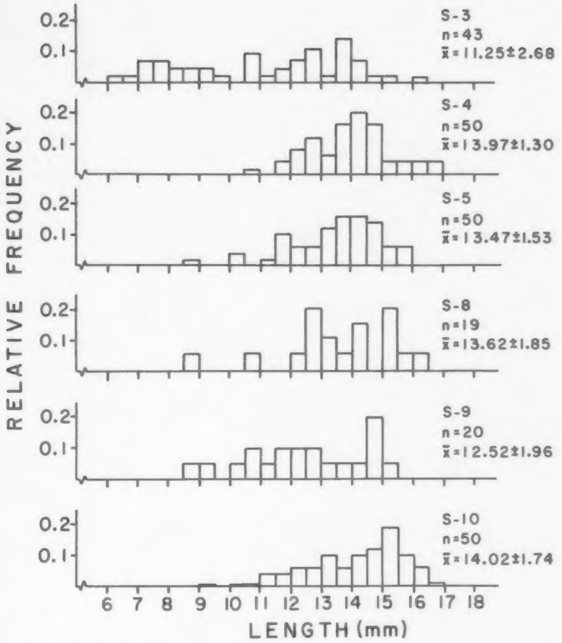

FIG. 7. Length–frequency distributions of smelt larvae captured at stations sampled in the St. Lawrence middle estuary, June 8, 1982; n = number measured, $\bar{X}$ = mean ± SD.

sampled at ESS-I and ESS-III (shallow-water stations) were larger than those captured offshore (ESS-II), during both 48-h series, suggesting that larger larvae occupy shallower water, near the shore, whereas smaller larvae are more readily dispersed offshore.

Sampling in the St. Lawrence middle estuary revealed that smelt larvae are transported to the northern portion of this zone (Fig. 6). The departure of larvae from the south channel must represent real lateral displacement, as no spawning sites occur along the north shore of the middle estuary (Fréchet et al. 1983). Furthermore, the comparison of length–frequency distributions of larvae captured at S-3 and S-10 (Fig. 7) during the first sampling survey reveal the smallest and youngest larvae present at S-3 (upstream, south shore) and the oldest and largest larvae present at S-10 (downstream, offshore), suggesting that smelt larvae are dispersed from the south to the center and northern portion of the middle estuary while they are transported downstream. The great range of larval sizes observed at all stations during the sampling surveys (Fig. 7, 8) and the high concentrations of larvae observed in this zone relative to the south shore (Fig. 6) suggest that different groups of smelt larvae emerging from different natal rivers (e.g. Ouelle River, Fig. 1) at different times are mixed together and remain in this area.

Mechanisms Controlling Distribution

The distribution of smelt larvae in the Boyer River is characterized by the accumulation of larvae at the river's mouth and the introduction of patches of larvae into the estuarine water mass every 24 h. The subsequent downstream transport of smelt larvae appears slower than the advection of the water mass. To explain these observations, we propose the following mechanisms.

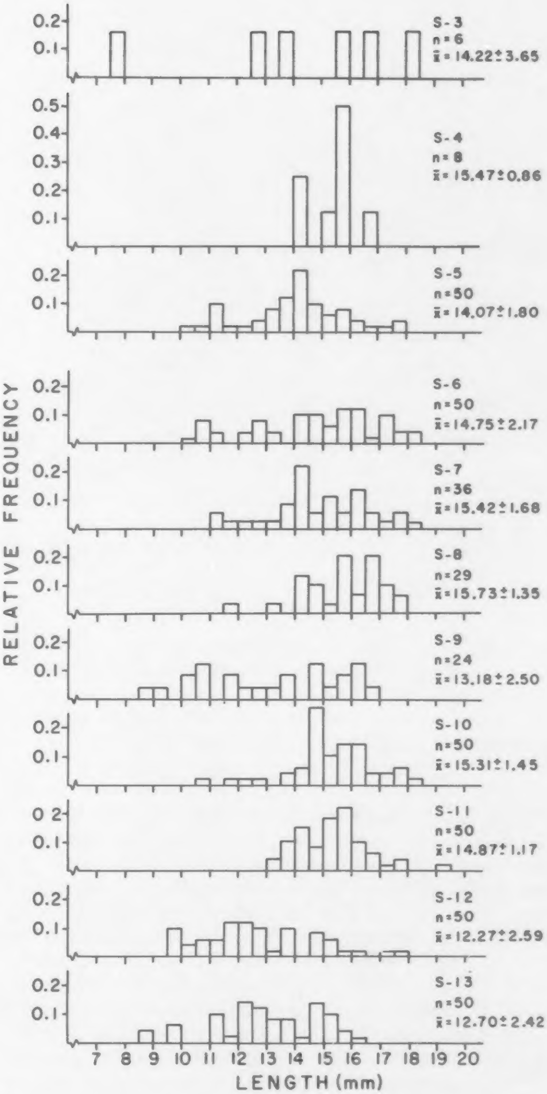

FIG. 8. Length–frequency distributions of smelt larvae captured at stations sampled in the St. Lawrence middle estuary, June 12, 1982; n = number measured, $\bar{X}$ = mean ± SD.

Possibly stimulated by an increase in temperature, the larvae emerge from the spawning ground at night and are transported through S-II (Fig. 1) by the fast and turbulent flow of this section. Downstream (S-I), the lower velocity and greater depth slows the drift of larvae to a point where negatively buoyant yolk-sac larvae may sink to the bottom and stay there during the day. As there is a continuous flux of larvae from upstream (S-II), this process may be responsible for the observed accumulation of larvae in the downstream section of the river. At dusk and during darkness, the larvae rise from the river bed, thus contributing to the 24-h periodicity in larval flushing. The waters of the Boyer River are highly turbid, and since there is no significant relation between river flow and larval abundance at the stations, we conclude that daytime net avoidance by

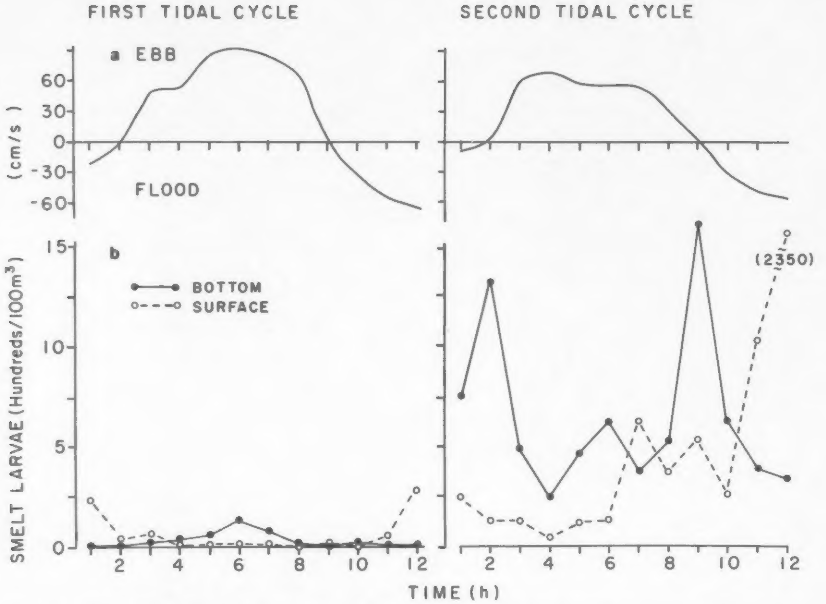

FIG. 9. Results of both 12-h stationary sampling series conducted in the St. Lawrence middle estuary on June 9, 1982 (first tidal cycle), and on June 13, 1982 (second tidal cycle). (a) Tidal – current speed curves; (b) density of smelt larvae in surface and bottom tows.

larvae does not occur and the pattern observed represents real displacement of the larvae in response to light conditions.

Swimming activity of newly hatched, yolk-sac fish larvae has been reported recently and related to different environmental factors. Peterson et al. (1980) demonstrated that yolk-sac tomcod (*Microgadus tomcod*) larvae actively swim to the surface to fill the swim bladder, which must be filled within 24 h of hatching. Smith et al. (1978) reported diel vertical displacement for recently hatched yellowtail flounder (*Limanda ferruginea*) larvae, the amplitude of diel movements increasing with size of larvae. Hunter (1972) observed swimming activity in 0- to 3-d-old anchovy (*Engraulis mordax*) and suggested a respiratory function for the swimming burst of yolk-sac larvae. Thus, although the swimming capability of yolk-sac fish larvae is limited (Braum 1978), we propose that even weak diel vertical displacement by smelt larvae, relative to the shallow waters of Boyer River, could be significant in regulating their aggregation at the river's mouth and subsequent dispersion from the river.

Sampling in Anse St-Vallier provides evidence that the vertical position of smelt larvae in the water column is responsible for their slow downstream dispersion. The first 48-h series at ESS-II revealed that the vertical position of smelt larvae is determined by light conditions and tidal current direction. To verify if net avoidance by larvae might be responsible for this observed day/night distribution, we compared the length–frequency distribution of larvae captured at ESS-II for day and night samples assuming that net avoidance would also result in larger larvae being captured at night. As no significant differences ($P > 0.05$) were found, we conclude that smelt larvae execute real vertical displacement in response to light condition as originally reported by Rogers (1940).

Although the 48-h series at the fixed station does not permit us to distinguish clearly between day/night and tidally induced behavior, the results suggest that the transport of smelt larvae in the estuary of the St. Lawrence is slowed by the observed tendency of larvae to remain in the deeper portion of the water column during ebb tides and by ascending the water column during flood tides. In the well-mixed region of Anse St-Vallier (Fig. 1), larvae may face weaker current speeds as they descend towards the bottom during ebb tides and thus reduce the extent of downstream transport. The efficiency of this behavior should be a function of the developmental stage of the larvae, as larger, stronger larvae show greater swimming ability (Blaxter 1969). Evidence in support of this is provided by the observation that smaller larvae are transported more readily out of Anse St-Vallier than are larger larvae.

We are unable to determine whether the vertical movement of smelt larvae related to tidal currents observed in Anse St-Vallier results from active or passive mechanisms. Henri et al. (1985) proposed that yolk-sac herring (*Clupea harengus harengus*) larvae, being negatively buoyant, tend to sink in slack water and are vertically transported by turbulence resulting from tidal currents. Such vertical transport would be more pronounced during the flood due to the deep currents experienced at the beginning of the flooding tide. Thus, as for the model presented by de Wolf (1973), the pattern of dispersion of organisms parallels the distribution of particulate matter in the water column and does not require any speculation concerning active swimming capabilities of young larvae. In our study, however, the diel vertical movements exhibited by young smelt larvae in Anse St-Vallier influence tide-related vertical movements and indicate that young larvae are capable of active swimming. Thus, we propose that larval behavior must be considered when dealing with the initial stages of smelt dispersion.

The interaction between estuary hydrodynamics and larval behavior proposed as the mechanism responsible for the observed drift pattern of smelt larvae in the upper section of the middle estuary does not prevent the net downstream dispersion of the larvae. However, smelt larvae apparently are confined to the middle estuary and are not found downstream of Ile aux Coudres (Able 1978). Furthermore, we have demonstrated that this accumulation and retention occurs mainly in the northern section of the middle estuary as evidenced by the downstream and lateral displacement of the larval abundance maximum revealed by the surveys conducted in the estuary (Fig. 6).

Although the first sampling survey revealed the oldest and largest larvae downstream and offshore (Fig. 7), the length-class frequencies of smelt larvae measured during the second survey (Fig. 8) are not in accordance with the south–north displacement observed in larval abundance. This observation may be due to differential transport time of larvae from different areas of the south shore to the northern middle estuary. For example, the sampling in Anse St-Vallier revealed an onshore–offshore gradient of larval mean length, with smaller larvae being captured offshore (Fig. 5). As the larvae move downstream during the ebb, larval patches on the offshore margin of the south channel are possibly transported through the center and northern portion of the estuary following the circulation pattern of this region, whereas the larvae closer to the south shore may continue their drift downstream following the south channel. Without knowing the details of the circulation throughout the entire area, the rate of cross-estuary transport cannot be estimated for every larval patch. In general, however, the maximum of larval abundance progressively moves northwards across the estuary (Fig. 6).

The distribution of smelt larvae observed in the present study conforms to the distribution of particulate suspended matter (PSM) in this region described by d'Anglejan (1981). He observed that tidal phase differences across the estuary, due to differences in bathymetry between the north and south channel, create strong shears at the turn of the tide on the crest of the English Bank (Fig. 1). This facilitates the cross-channel transport of PSM from the south into the north channel. Ouellet and Trump (1979) also reported a south to north displacement of the water mass in the upper section of the middle St. Lawrence estuary at the turn of the tide.

Larvae sampled in this area also exhibit vertical displacements related to tidal currents (Fig. 9), concentrating near the bottom during ebb and moving up into the water column during flood tide. As the northern upstream section of the middle estuary is partially mixed and exhibits a net upstream flow of salt water along the bottom (Ouellet and Trump 1979), we propose that the vertical displacements exhibited by smelt larvae in combination with the two-layer circulation system of this area result in the retention of smelt larvae upstream of Ile aux Coudres. Futhermore, as larvae sampled on this occasion were large (>12 mm), the efficiency of this behavior should be greater as swimming ability develops with increasing size.

In summary, the dispersion and resultant distribution of smelt larvae appears to be the result of a combination of the dominant physical oceanographic features of the middle estuary and the behavior of larvae. The slow downstream transport of larvae, apparently due to vertical displacements in response to tidal state and light conditions, results in the majority of smelt larvae attaining sizes at which they may exploit more efficiently the two-layer circulation system of the northern section of the middle estuary. The vertical position of yolk-sac and immediate post yolk-sac larvae appears to be controlled by a combination of active phototaxic movements and tide-related movements that may be active or passive. The relative contributions of active and passive mechanisms of vertical displacement are unknown.

Acknowledgments

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Morphology and Systematics of the Nemertean *Pseudocarcinonemertes homari* (Hoplonemertea: Monostilifera) from the American Lobster, *Homarus americanus*

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Uhazy, L. S., D. E. Aiken, and A. Campbell. 1985. Morphology and systematics of the nemertean *Pseudocarcinonemertes homari* (Hoplonemertea: Monostilifera) from the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 342–350.

Our study of the morphology and systematics of the nemertean *Pseudocarcinonemertes homari* Fleming and Gibson, 1981 is based on specimens removed from the damaged egg masses of American lobsters, *Homarus americanus*, caught in the type locality at Grand Manan, N.B., in the Bay of Fundy and nearby Passamaquoddy Bay. Morphological characteristics and measurements of males, females, and developmental stages, obtained through examination of live and preserved nemerteans plus stained histological sections, revealed differences and provided additional indications of variability in measurements of taxonomic characters when compared with the original description. Specifically, female nemerteans are longer and slightly wider than males; the rhynchodael opening is subterminal; sensory bristles occur lateral to the rhynchodael and anal openings; cephalic furrows are observable on living specimens; the combined stylet–basis length is longer than reported and stylet length appears a stable character; the bulbous or sacculate foregut joins to a distinct pyloric tube; ova are large, 260 × 251 μm in length and width; and larvae retained in the membranous brood sac lack anterior and posterior cirri or tufts. Comparison of characters that define *Pseudocarcinonemertes* and differentiate it from *Carcinonemertes* with those defining free-living hoplonemerteans strongly supports its removal from the family Carcinonemertidae to the family Tetrastemmatidae.

La présente étude de la morphologie et de la systématique du némertien *Pseudocarcinonemertes homari* Fleming et Gibson, 1981 est basée sur des spécimens prélevés de masses endommagées d'œufs de homards d'Amérique, *Homarus americanus*, capturés dans la localité-type, soit Grand-Manan (N.-B.), dans la baie de Fundy et la baie Passamaquoddy avoisinante. Les caractéristiques morphologiques et les mesures effectuées sur les mâles, les femelles et les stades larvaires (examen de spécimens vivants et préservés et coupes histologiques colorées) ont révélé des différences et des preuves additionnelles de la variabilité des caractéristiques taxonomiques par rapport à la description originelle. Plus précisément, la femelle est plus longue et légèrement plus large que le mâle ; l'ouverture du rhynchodeum est subinfère ; des soies sensorielles sont présentes en position latérales à l'ouverture du rhynchodeum et de l'anus ; des sillons céphaliques sont présents chez les spécimens vivants ; la longueur combinée du style et de sa base est plus longue que celle signalée et la longueur du style semble être un caractère stable ; le stomodeum bulbeux ou sacculé s'unit à un tube pylorique distinct ; les ovules sont gros, mesurant 260 μm de longueur et 251 μm de largeur ; et les larves gardées dans la poche incubatrice membraneuse n'ont pas de cirres ou mèches antérieures et postérieures. Une comparaison des caractéristiques qui définissent *Pseudocarcinonemertes* (et le différencient de *Carcinonemertes*) avec celles qui identifient les hoplonémertiens indépendants étaye fortement le bon retrait du premier de la famille Carcinonemertidae et son inclusion dans la famille Tetrastemmatidae.

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Fleming and Gibson (1981) described the nemertean *Pseudocarcinonemertes homari*, an ectohabitant on the American lobster (*Homarus americanus*), and placed it in the hoplonemertean family Carcinonemertidae, a monogeneric family (*Carcinonemertes*) with all species parasitic or ectohabitant on crabs (Humes 1942; Gibson 1982). After a preliminary study of specimens from the type locality, the assignment of *P. homari* to this family was questioned by Aiken et al. (1983). In this article we present results of a detailed study of *P. homari* morphology and a new interpretation of its systematic position. Current knowledge on biology, feeding habits, and distribution of *P. homari* is presented in companion papers (Aiken et al. 1985; Waddy and Aiken 1985; Brattey et al. 1985).

Materials and Methods

Specimens of the nemertean *P. homari* were obtained from the egg masses of six lobsters, three of which were caught by commercial fishermen in traps set at depths of 170–210 m off Grand Manan in the Bay of Fundy, the type locality, while the others were taken with otter trawls at 106 m in Western Passage, Passamaquoddy Bay. In all cases the unusual appearance of the lobster egg masses prompted their transport alive to the Biological Station, St. Andrews, N.B., where portions of the degenerate lobster brood containing many adult *P. homari* and intermediate developmental stages were removed.

Live nemerteans were maintained in stacking dishes containing seawater at 4°C. For microscopic examination as live wet mounts and for measurements they were anesthetized with amyl alcohol (1 mL/100 mL seawater). Specimens slowed by coverslip pressure were also examined. Specimens for permanent whole mounts were either fixed in hot ethyl alcohol – formalin – acetic acid (AFA) and stained with Semichon's acetocarmine, or fixed in hot 10% glycerol in 70% ethyl alcohol and cleared in glycerol. Live nemerteans and lobster tissues for histological examination were fixed in 10% formalin, embedded in paraplast, sectioned at 7 μm, and stained with Ehrlich's haematoxylin and eosin. Measurements were made with the aid of a drawing tube or eyepiece micrometer.

Representative specimens and a series of prepared slides of serially sectioned specimens are deposited at the National Museum of Natural Sciences, Invertebrate Collection (Parasites), Ottawa, Ont. K1A 0M8. Others are deposited at the Atlantic Reference Center, Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B. E0G 2X0.

Results and Discussion

Fleming and Gibson (1981) described *P. homari* as an ectohabitant and parasite of American lobsters caught off Grand Manan in the Bay of Fundy. In the following we include additional descriptive material and a new systematic interpretation; this is intended as an extension of their presentation. In succeeding sections these features and interpretations are presented in detail.

Pseudocarcinonemertes Fleming and Gibson, 1981

Diagnosis

Hoplonemertea, Monostilifera. Small, cylindrical nemerteans slightly flattened dorsoventrally with rounded anterior and slightly tapered rounded posterior end. Frontal organ dorsal to opening of rhynchodaeum, cephalic glands large. Four ocelli positioned on the anterior end form the corners of a trapezoid. Conspicuous cerebral sense organs (= cerebral organ) in front of second pair of ocelli, directed anteriolaterally and opening ventrally. Bilobed cerebral ganglia connected by narrow dorsal and stouter ventral commissures. Bilateral nerve cords ventrolateral adjacent to alimentary tract, internal to the musculature of body wall and prominent submuscular glands. Submuscular glands associated with all surfaces, with greatest development on the ventral and lateral surfaces. Proboscis with three chambers, proboscis sheath (rhynchocoel) extends posteriorly about half the nemertean total length. Anterior chamber short and protrusible. Septum between anterior and small muscular middle chambers armed with a central stylet and two lateral accessory stylet pouches. Posterior chamber glandular and longer than the anterior chamber. Alimentary tract consists of a short esophagus, sacculate stomach with a distinct pyloric tube, intestinal cecum, and intestine. Lateral cecal and intestinal diverticulae (pouches) prominent, unbranched, and lobular. Sexes separate and gonads regularly distributed between the cecal and intestinal diverticulae. Ectoparasite on *Homarus americanus*.

Pseudocarcinonemertes homari Fleming and Gibson, 1981

Description

Female (based on nine mature specimens, each containing at least one large ovum). Body ciliated, yellow to orange in color. Length 7.2 mm (5.7–8.7), and up to 12 mm when fully extended. Maximum width at posterior end of proboscis sheath 0.8 mm (0.5–1.0). Four ocelli anterior to prominent bilobed cerebral ganglia, first pair 230 (190–300) and second pair 290 (200–360) from anterior end. Distance between ocelli in each pair 215 (150–260) and 290 (200–360), respectively. Large paired cerebral sense organs just anterior to second pair of ocelli (Fig. 1), cerebral canal directed anteriolaterally, and opening ventrally by distinct sensory pits (Fig. 2). Cephalic furrows (Fig. 3) meet dorsomedially and directed posteriad just posterior to cerebral ganglia, 520 (500–750) from anterior extremity. Ventrolateral nephridiopores associated with cephalic furrow. Opening to rhynchodaeum subterminal, marked by short ciliated groove and bordered laterally by bristles (Fig. 4). Bristles irregularly distributed on dorsal surface to level of cephalic furrow. Frontal organ dorsal to rhynchodael opening (Fig. 5) and cephalic glands prominent. Functional proboscis dorsal to alimentary tract, with proboscis sheath attaching to dorsal body wall by muscular ligament 3.5 mm (2.6–4.5) from anterior extremity. Proboscis with three chambers; anterior chamber when everted covered by prominent protuberances (Fig. 6) containing glandular cells (Fig. 7); septum between anterior and middle chambers supports a central stylet, slightly smaller than the basis (41% of combined length), and two lateral accessory stylet pouches (Fig. 8). When everted, proboscis passes between commissures of bilobed cerebral ganglia (Fig. 5, 15); armature at distal end with stylet protruding (Fig. 9). Small middle chamber muscular, often containing small circular vesicles (Fig. 9). Posterior chamber large and glandular. Short esophagus joins rhynchodaeum just anterior to cephalic ganglia, passes below ventral commissure and connects to a sacculate stomach with a distinct pyloric tube. Large intestinal cecum extends anteriorly ventral to pyloric tube and abuts with foregut

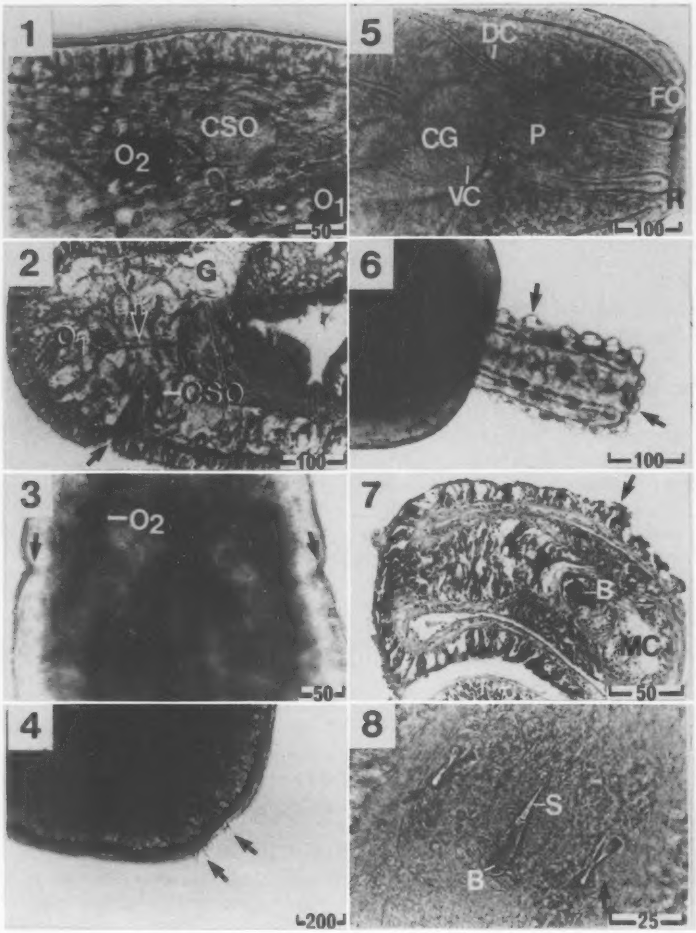

Fig. 1. Dorsal view of a live specimen showing a cerebral sense organ (CSO) anterior to the second ocellus (O_2). Fig. 2. Longitudinal section through a cerebral sense organ showing the canal and ventrolateral sensory pit (arrow). Note the dorsal cephalic glands (G) and the nerve tract (arrow) extending from the cerebral ganglion to the first ocellus (O_1). Fig. 3. Dorsal view of a live specimen showing the lateral aspect of the cephalic furrows (arrows). Fig. 4. Dorsal view of a live specimen showing anterior bristles (arrows) associated with the rhynchodeal opening. Fig. 5. Sagittal section through the cephalic region of a specimen cleared in glycerol. Note the partially everted proboscis (P) passing between the dorsal (DC) and ventral commissures (VC) of the cerebral ganglia (CG), the opening of the rhynchodaeum (R), and the frontal organ (FO). Fig. 6. Dorsal view of a live specimen showing the protuberances (arrows) on the partially everted proboscis. Fig. 7. Saggital section of a partially everted proboscis showing the glandular epidermis (arrow) of the protuberances. Note the basis (B) of the stylet and the middle chamber (MC) of the proboscis. Fig. 8. Dorsal view of a live specimen showing the proboscis armature. Note the conical stylet (S) and its flange inset on the basis, and the lateral accessory stylet pouches (arrows). Scale units for Fig. 1–8 in micrometres.

(Fig. 10). Intestine long, lateral cecal and intestinal diverticulae unbranched and lobular (Fig. 11). Anus terminal, bordered laterally by bristles (Fig. 12). Ovaries numerous and regularly distributed between cecal and intestinal diverticulae; dorsolateral, lateral, and ventral in position. Ova large, yellow or white, at times numerous and packing the body of the nemertean.

Male (based on 10 mature specimens). Orange in color. Similar in gross morphology to female other than: length 4.9 mm (3.5–6.6), and up to 9 mm when fully extended. Maximum width at posterior end of proboscis sheath 0.6 mm (0.4–1.0). First pair of ocelli 170 (120–210), second pair 310 (190–390) from anterior end. Distance between ocelli in each pair 176 (130–200) and 242 (150–310), respectively. Cephalic furrow 470 (400–590) from anterior extremity. Proboscis sheath ending 2.6 mm (2.1–3.2) from anterior end. Testis and

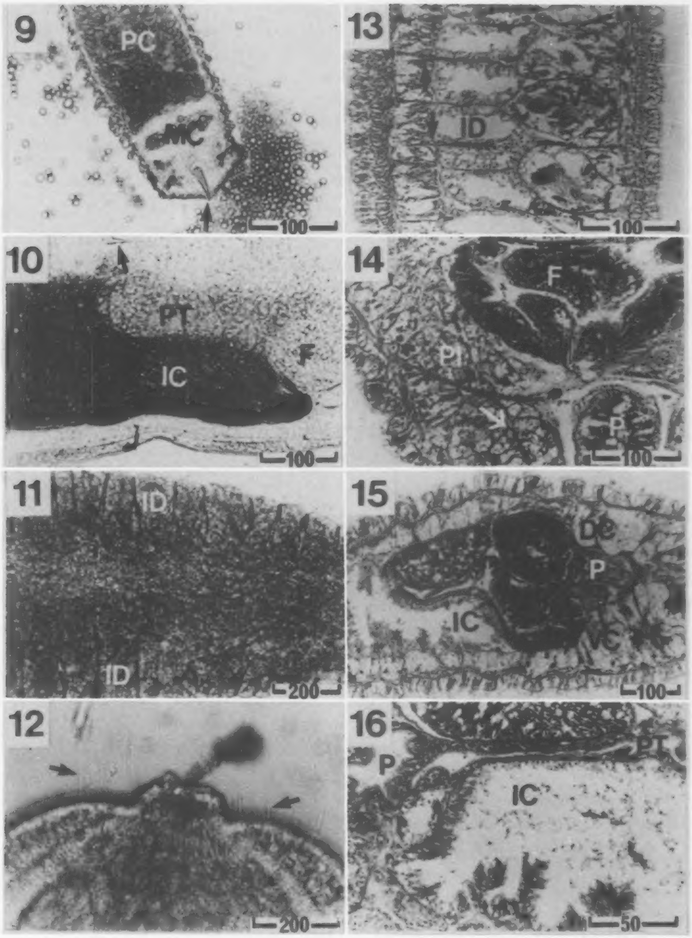

FIG. 9. Dorsal view of a live specimen with a fully everted proboscis. Note the terminal position of the stylet (arrow) and the spherical vesicles present in the posterior chamber (PC), middle chamber (MC), and external to the proboscis. FIG. 10. Lateral view of a live specimen showing the intestinal cecum (IC) ventral to the pyloric tube (PT) and abutting the foregut (F) portion of the stomach. Note the lateral cecal diverticulae and the stylet (arrow) of the inverted proboscis dorsal to the alimentary tract. FIG. 11. Dorsal view of a live specimen showing the intestine with lateral unbranched diverticulae (ID). FIG. 12. Dorsal view of a live specimen showing the terminal anus and lateral bristles (arrow). FIG. 13. Longitudinal section through a male showing a lateral view of the ventral testis and seminal vesicle (SV). Note the dorsoventral muscle fibers (arrows) passing between the intestinal diverticulae. FIG. 14. Longitudinal section lateral to midline showing the proboscis insertion (PI) and an anterior extension of this musculature (arrow). Note the proboscis (P) and folded foregut. FIG. 15. Near sagittal section through the intestinal cecum which abuts the foregut portion of the stomach. Note the proboscis passing between the ventral (VC) and dorsal commissures (DC) of the cerebral ganglia. FIG. 16. Longitudinal section of the stomach showing the pyloric tube extending posteriorly between the proboscis and intestinal cecum. Scale units for Fig. 9–16 in micrometres.

seminal vesicles regularly distributed between cecal and intestinal diverticulae, ventral in position (Fig. 13).

Comparison of Descriptions of *Pseudocarcinonemertes homari*

In contrast with the published description (Fleming and Gibson 1981), we observed a sexual dimorphism, with females longer and slightly wider than males and differences in several of the external features. Anesthetized male and female *P. homari* were on average longer than reported and when fully extended and gliding across a smooth surface; males are up to 9 mm long, while females are up to 12 mm, considerably longer than the reported 8 mm.

The four ocelli situated on the anterior end of *P. homari* are

TABLE 1. Comparison of the stylet and basis (mean ± 1 SD, range in parentheses) in mature female and male *Pseudocarcinonemertes homari* from *Homarus americanus*.

	n	Total length (µm)	Stylet length (µm)	Basis length (µm)	Stylet:basis ratio
Female	5	74.9±5.1 (68.4–79.8)	32.3±1.3 (30.4–34.2)	48.3±5.3 (42.8–54.2)	0.674±0.07 (0.595–0.754)
	3[a]		21.0±0.7 (20.2–21.4)	44.5±7.9 (39.7–53.6)	0.480±0.07 (0.389–0.531)
Male	5	66.8±6.4 (57.0–72.2)	31.2±2.2 (28.5–34.2)	40.5±5.4 (32.2–45.6)	0.777±0.07 (0.708–0.882)
	2[a]		21.5±7.1 (16.4–26.5)	37.8±5.4 (34.0–41.6)	0.587±0.22 (0.394–0.779)

[a] Computed data presented by Fleming and Gibson (1981).

subintegumental in position and observable under low power magnification. In both sexes they are uniform in size (approximately 30 µm in diameter) and characteristically form the corners of a trapezoid. Fleming and Gibson (1981) implied that ocelli number might not be a stable taxonomic character. However, our observations on a great many specimens indicate four ocelli is a stable character in *P. homari*.

The opening of the rhynchodaeum is subterminal in position, not terminal as indicated by Fleming and Gibson (1981), and marked by a ciliated groove. In live specimens, apparent sensory bristles, extending beyond the limit of the dense cilia which generally cover the integument, are grouped on either side of the rhynchodael opening. When viewed from the lateral perspective, similar individual bristles were irregularly distributed along the dorsal surface of the nemertean to the level of the cephalic furrows. Fleming and Gibson stated: "The head is rounded, without cephalic furrows." However, on live specimens of *P. homari*, cephalic furrows located posterior to the cerebral ganglia at the level of the most anterior portion of the stomach were observed (Fig. 3). Groups of bristles similar in appearance to those associated with the anterior end were also restricted to the posterior terminus lateral to the anus. These bristles and the cephalic furrows were not observed in preserved whole mounts and sectioned specimens, which may explain their absence from the description provided by Fleming and Gibson.

The prominent proboscis is essentially as described in the original description. The short, protrusible anterior chamber constitutes about 11% of total body length, and the glandular posterior chamber is longer and retained in the proboscis sheath. The latter has a length of 49 and 52% of total body length in females and males, respectively. However, we found the stylet and its basis to be longer than reported (Table 1). From the report of Fleming and Gibson (1981), mean stylet and basis lengths (based on the combined measurements of two males and three females) were 21.2 and 41.8 µm, respectively. This contrasts with mean measurements of 31.7 and 44.4 µm from this study. In comparing the combined stylet–basis lengths and basis lengths between five mature male and female *P. homari*, it is apparent that this structure and its basis are larger in females ($t = 2.21$, $p < 0.05$ and $t = 2.39$, $p < 0.05$, respectively). There was, however, no difference in stylet length ($t = 0.97$, $p > 0.05$). As such, mean stylet to basis ratios were 0.674 for females and 0.777 for males. It is readily apparent that stylet length is a stable characteristic, while length of the basis is not. This latter structure is positioned in what appears to be granular synthetic tissue and may well increase in size allometrically with increasing nemertean size. Fleming and Gibson reported the basis as with or without a median waist. In examination of many specimens, we found the shape of the basis to be much more polymorphic.

Fleming and Gibson (1981) also reported finding one male that had six accessory pouches associated with the armature of the proboscis. We never observed more than two accessory stylet pouches. In general, three stylets were present in each lateral accessory stylet pouch, although the number varied and as many as five were seen in some animals ($n = 44$).

The muscular middle chamber of the proboscis, posterior to the septum supporting the armature, frequently contained spherical vesicles (Fig. 9). These are apparently secreted by the glandular posterior chamber, for similar vesicles were observed in the anterior portion of this chamber. With protrusion of the anterior chamber, contraction of the middle chamber facilitated the passage of these vesicles through the septum to the outside via a duct ventral to the basis of the stylet. The function of these vesicles is unknown; however, it is possible that they serve in concert with the protruding stylet and function in extracorporeal digestion following penetration of the lobster egg membranes.

Serial longitudinal and transverse tissue sections revealed typical monostiliferous hoplonemertean integument. The ciliated epidermis, containing many irregularly distributed glandular cells, appeared variable in thickness. In the region of the proboscis sheath, the ventral epidermis is thicker (43.7 µm; range 34–56) than the dorsal surface (34.3 µm; range 26–46). The subepidermal tissues consist of outer circular and inner longitudinal muscle layers, each measuring about 10–15 µm in thickness. However, in the cephalic region anterior to the dorsal origin of the proboscis insertion and ventrally anterior to the canals of the cerebral sense organs, the body wall musculature is reduced in thickness. Anterior to the proboscis insertion (Fig. 14) is a meshwork of longitudinal muscle fibers suggestive of a precerebral septum (Kirsteuer 1974). There are also many oblique fibers that extend from the longitudinal musculature of the body wall to the surface of the rhynchodaeum and the anterior extremity. The origin of the proboscis insertion, observed in specimens cleared in glycerol and longitudinally sectioned, is positioned such that it could be in association with the cephalic furrows observed in live specimens. In live *P. homari* the cephalic portion is capable of retraction and lateral movement, and appears hinged at the cephalic furrow. Bristles lateral to the rhynchodael opening and on the dorsal surface suggest that these cephalic movements serve sensory functions.

It was also apparent that the nephridiopores of the "rudimentary excretory system" (Fleming and Gibson 1981) are associated with the furrow.

The submuscular region is characterized by much reduced parenchymal tissues and large lobular submuscular glands. Parenchymal tissues are found in the cerebral region adjacent to the alimentary canal where they contained the excretory system, around the ventrolateral nerve cords and lateral blood vessels, and around the mid-dorsal blood vessel that lies between the proboscis sheath and the intestine. The submuscular glands are generally distributed throughout the nemertean but are reduced in size anterior to the cerebal ganglia and in the dorsal and dorsolateral regions. The cephalic glands of the frontal organ dominated the dorsal submuscular space in the cephalic region of the nemertean. It is apparent that the ciliated ventral surface functions with the well-developed ventral and ventrolateral submuscular glands to form an adhesive dermal surface that facilitates movements of *P. homari* through the lobster egg mass and across exposed external surfaces.

A short esophagus lined by a nonglandular, sparsely ciliated epithelium joins the rhynchodaeum anterior to the cerebral ganglia. These epithelial cells and the remainder of those in the alimentary canal are positioned on a delicate basement membrane. The esophagus passes below the ventral commissure and joins the stomach. Fleming and Gibson (1981) described this organ as a "tubular stomach opening into the dorsal wall of the intestine without distinct pyloric tube, [and a] comparatively short, rather cone-shaped chamber ... [which posteriorly] narrows to form a short, slender duct which opens into the dorsal surface of the intestine ... but a distinct pyloric tube as such is missing." In contrast, our observations on live *P. homari* indicated that the anterior portion of the stomach is a bulbous or sacculate structure with a distinct pyloric tube that extends posterior ventral to the proboscis and dorsal to the intestinal cecum (Fig. 10, 15) to join with the dorsal aspect of the intestine (Fig. 16, 17) (Coe 1943; Gibson 1972; Kirsteuer 1974).

In sectioned materials the foregut was observed to be deeply folded and lined by a ciliated pseudostratified columnar epithelium containing many glandular cells (Fig. 18). Glandular cells were common in the anterior portion of the ciliated cuboidal epithelium of the pyloric region, but less common in the posterior tubular portion of this organ. Cilia on the free surfaces of this organ form a prominent brush border.

The spacious cecum extends well anterior and ventral to the pyloric tube to abut with the foregut. It and the much longer intestinal portion of the alimentary tract have prominent, regularly distributed, lateral, unbranched but lobular diverticulae. At times the lobular appearance was less obvious, perhaps due to the presence of ingesta. It is interesting that in juvenile *Pseudocarcinonemertes* recently released from the membranous brood sac, alimentary diverticulae were not observed.

The cecum, intestine, and their diverticulae are lined with a foliate columnar epithelium whose free surfaces appear to coalesce (Fig. 19, 20). This epithelium is raised into minor ridges, apparently increasing the absorptive surface area of these organs. Sparsely distributed cecal and intestinal cilia, characteristic of hoplonemerteans (Gibson 1972), were not observed. However, the coalescence of the free surfaces was suggestive of clusters of cilia observed on preserved ciliophora. If such is the case, the gross morphology of cilia in the gastric brush border differs significantly from that in the remainder of the alimentary tract. In the rectal region the epithelium is cuboidal and contains numerous goblet-like cells (Fig. 21).

Fleming and Gibson (1981) described the gonads of female *P. homari* as irregularly distributed between the intestinal diverticulae, but we found them to be regularly distributed. They lie between the submuscular glands and the wall of the alimentary canal and extend from the level of the intestinal cecum posterior to the rectum. They are dorsolateral, lateral, and ventral in disposition and appear supported by the dorsoventral longitudinal muscles that pass between the cecal and intestinal diverticulae. Since their development is not synchronous, ova in various stages of development contribute to the impression of an irregular distribution. Small ova, diameter 5–50 μm in tissue section, are regularly placed between the cecal and intestinal diverticulae, while larger ova, diameter 190–240 μm in tissue section, displace the alimentary tract and ventrolateral nerve cord and hence give the impression of an irregular distribution. The large size of these ova contrasts Fleming and Gibson's (1981) indication of ripe ova with diameters ranging from 135 to 140 μm.

Developing ova appear to increase in size through the coalescence of homogeneously stained dense vesicles, which appear to emanate from the ovarian epithelium (Fig. 22). Large ova apparently ready for oviposition have several round basophilic bodies within the nucleus, close to the nuclear membrane (Fig. 22, 23), and a basophilic outer membrane. An oviduct, characterized by an infolding of the body musculature and the presence of a distinct dilation, is associated with these ova (Fig. 23).

In male *P. homari*, the testes and accompanying seminal vesicles are ventrolateral in position and regularly placed along the alimentary tract between the cecal and intestinal diverticulae. In tissue sections they measured 117 μm (94–157) by 78 μm (53–94) in length and width. An efferent duct leads from the seminal vesicle of each testis through the body wall (Fig. 24). As a function of this arrangement, the testes often appeared to be doubled, a fact noted by Fleming and Gibson (1981). Spermatozoa, also called nematosperms, are flagellated and in section tissues measured 24–34.5 μm in length.

Copulation and oviposition were not observed. However, eggs are deposited in large, readily observed membranous brood sacs (termed cocoons by Fleming and Gibson 1981) affixed to nonplumose setae on the abdominal pleopods and membranes of lobster eggs (see Aiken et al. 1985). The brood sac consists of a densely staining membrane, and in 10 examined, a mean of 39 eggs (range 30–47) was observed. The eggs are subspherical in shape, length 260 μm (221–313), width 251 μm (211–379) ($n = 25$). Newly hatched larvae, retained in the broodsac, are ciliated, lack anterior and posterior cirri, and have ocelli and visible internal structures including the proboscis.

Comparison of *Pseudocarcinonemertes* and *Carcinonemertes*

The uniqueness of the nemertean of the American lobster was indicated by Fleming and Gibson (1981), and subsequent study of symbionts from five species of crabs from Atlantic waters (Brattey et al. 1982) clearly demonstrates this specificity. The erection of *Pseudocarcinonemertes* gen. nov. is therefore defensible; however, we question Fleming and Gibson's placement of this genus in the monogeneric family Carcinonemertidae. In arriving at this placement, Fleming and Gibson referred to Humes (1942) revision in which the Carcinonemertidae were differentiated from the most closely related family, the Emplectonematidae, by five characteristics: (1) ectohabi-

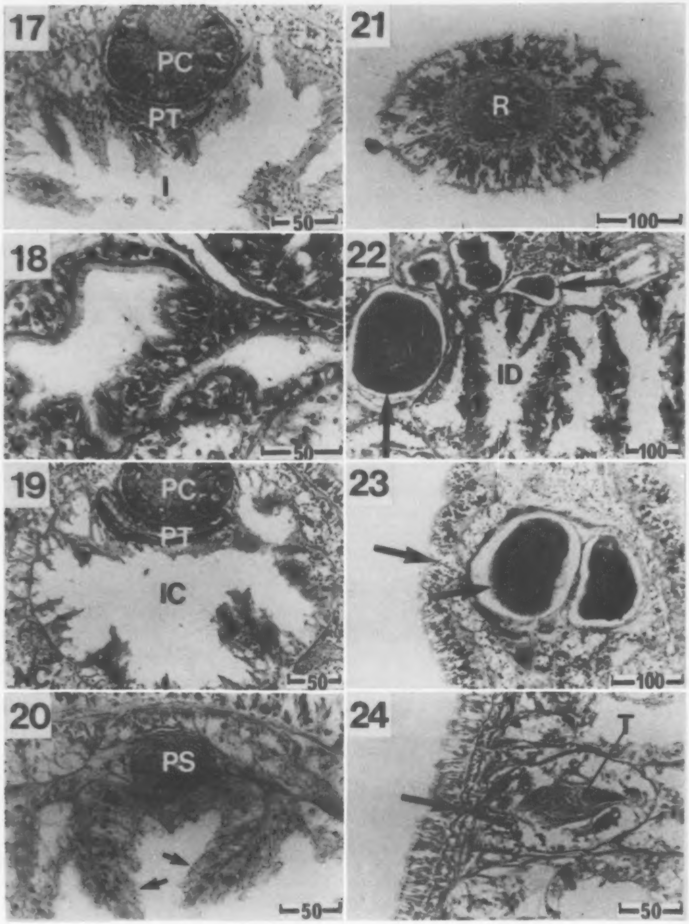

FIG. 17. Transverse section showing the union of the pyloric tube (PT) to the dorsal surface of the intestine (1). Note the posterior chamber (PC) of the proboscis. FIG. 18. Longitudinal section through the stomach showing the ciliated pseudostratified columnar epithelium of the folded foregut. FIG. 19. Transverse section through the intestinal cecum (IC), pyloric tube, and the posterior chamber of the proboscis. Note the ciliated cuboidal epithelium of the pyloric tube, the foliate appearance of the cecal epithelium, and the ventrolateral nerve cords (NC) adjacent to the cecal wall. FIG. 20. Transverse section through the intestinal region at the level of the posterior terminus of the proboscis sheath (PS). Note the foliate columnar epithelium (arrows) and the attachment of the proboscis sheath to the dorsal body wall. FIG. 21. Transverse section through the rectum (R). FIG. 22. Oblique frontal section through a female showing ova (arrows) in various stages of development. Note the distortion of the intestine, intestinal diverticulae (ID), the lateral nerve cord, and the basophilic bodies in the nucleus of the large ovum. FIG. 23. Oblique section through two ova showing the oviduct, an infolding of the body wall musculature (arrow). Note the membrane around the ovum (arrow) and the basophilic granules in the nucleus. FIG. 24. Longitudinal section through a male showing the testis (T), seminal vesicle, spermatozoa, and an efferent duct (arrow) passing through the ventral body wall. Scale units for Fig. 17–24 in micrometres.

tants of crabs; (2) one central stylet with no traces of accessory pouches or stylets; (3) no cerebral organ; (4) presence of Takakura's duct in males; and (5) massive development of both cephalic and submuscular glands.

Although Fleming and Gibson (1981) disregarded the differences between crabs and lobsters in this context, *Pseudocarcinonemertes* nevertheless displays only one of the five characteristics of Humes' (1942) diagnosis (well-developed cephalic and submuscular glands), and in our opinion does not qualify for inclusion in the family Carcinonemertidae. Failure of *P. homari* to qualify on points 2–4 of Humes' diagnosis was dismissed by Fleming and Gibson as indicative of a more primitive level of parasitism in this species. In their opinion, *Pseudocarcinonemertes* "... shares some of the adaptations to parasitism exhibited by *Carcinonemertes* (small proboscis, massive cephalic and submuscular gland development, an habitual association with a crustacean host) whilst retaining certain features (cerebral organs, accessory stylets and pouches in the proboscis) more typically associated with free-living hoplonemerteans." Therefore, they concluded that *Pseudocarcinonemertes* gen. nov. is more closely related to the genus *Carcinonemertes* than to any other hoplonemertean group and placed it in the family Carcinonemertidae.

In our opinion, this conclusion overlooks the systematic significance of the 10 major morphological characters (table II, Fleming and Gibson 1981) that differ between the genera. An examination of these plus the additional differences noted in this study clearly supports our contention.

Takakura's duct, a common posterior seminal vesicle formed from efferent testicular tubules and opening to the outside via the anus (Humes 1942), is unique to male *Carcinonemertes*. In marked contrast, *Pseudocarcinonemertes* has a short efferent duct extending from each testis through the body wall (Fig. 24).

The "small proboscis" indicated as a common feature is open to challenge. The proboscis in *Carcinonemertes* is much reduced in size. Based on data presented by Humes (1942), the combined lengths of the proboscis middle and posterior chambers in *C. epialti* is 4% of the nemerteans total length. It extends to about the posterior end of the stomach, has short, nonglandular anterior and posterior chambers, a much reduced proboscis sheath, lacks accessory stylet pouches, and is nonfunctional as a protrusible organ (see Humes 1942; Wickham 1978, p. 198, fig. 2). In *Pseudocarcinonemertes*, the proboscis extends well beyond the posterior limit of the stomach, has longer glandular anterior and posterior chambers, has two accessory stylet pouches, and a sheath extending up to 50% of the total length of the nemertean. The proboscis (or anterior chamber) is functional as a protrusible organ and alone is equal to about 11% of total body length. It is very different from that in *Carcinonemertes*.

The alimentary systems in the two genera are different and in the case of our study of *P. homari* different than previously reported (Fleming and Gibson 1981). *Carcinonemertes* has no pyloric tube and the stomach joins directly to the intestine, which has only rudimentary lateral diverticulae (Humes 1942; Coe 1943). *Pseudocarcinonemertes* has a distinct pyloric tube that joins to the intestine posterior to the intestinal cecum, and both organs have discrete lateral diverticulae.

Eggs produced by *Carcinonemertes* spp. are considerably smaller than those of *Pseudocarcinonemertes*. Humes (1942) reported fertilized eggs of *C. imminuta* to be 55 μm in diameter, while Roe (1979) found eggs of *C. epialti* to be 7–7.5 by 6–6.5 μm in diameter. These contrast with our finding that *Pseudocarcinonemertes* eggs have average lengths and widths of 260 by 251 μm. It is also of interest to note that although both have direct embryological development, differences exist in the morphology and behavior of the respective larvae. *Carcinonemertes* larvae have two ocelli, anterior and posterior cirri or tufts, and a rudimentary proboscis, and are free-swimming (Humes 1942; Wickham 1980; Stricker and Reed 1981). *Pseudocarcinonemertes* larvae, by contrast, have four ocelli, do not have anterior and posterior cirri or tufts, have a visible proboscis, and are not free-swimming at any point in their development.

Considering the above and the presence of a frontal organ, cerebral sense organs, mid-dorsal blood vessel, and excretory system in *Pseudocarcinonemertes*, it becomes clear that features used to differentiate between genera are characters that align *Pseudocarcinonemertes* with other free-living hoplonemerteans (Humes 1942; Coe 1943; Gibson 1972; Kisteuer 1974; Gibson 1982). If one considers Iwata's (1960) phylogenetic scheme for the Nemertea based on larval characteristics, the presence of a fully formed proboscis and absence of cirri or tufts would suggest that *Pseudocarcinonemertes* is more hoplonemertean in character than *Carcinonemertes*.

In summary, *Pseudocarcinonemertes* has the following characteristics that are atypical of the Carcinonemertidae: (a) four ocelli; (b) functional proboscis with a central stylet and lateral accessory pouches and a proboscis sheath extending about 50% of total body length; (c) cerebral sensory organs anterior to cerebral ganglia and the second pair of ocelli; (d) an alimentary tract with a pyloric tube, intestinal cecum, and distinct cecal and intestinal diverticulae; and (e) a nonplanktonic larval stage. In our opinion these characters more closely align this genus with free-living species of monostiliferous hoplonemerteans found in the family Tetrastemmatidae (after Coe 1905; 1943). This family is further developed by Freidrich (1955) and Gibson (1972, 1982), is polygeneric and seems a more plausible placement of the genus.

The Tetrastemmatidae are mostly small slender monostiliferans. The type genus *Tetrastemma* is a free-living marine subtidal and littoral nemertean. Characteristically the head is usually the same diameter as the body or somewhat wider and provided with inconspicuous transverse grooves (cephalic furrows). The tip of the head has circular, longitudinal, and retractor muscles. The precerebral septum is closed. Four ocelli are present, the lateral nerves have a single fiber core, and the position of the cerebral sense organs is anterior to but close to the cerebral ganglia. Cephalic glands are variably developed and sometimes extend beyond the cerebral ganglia. The proboscis, usually armed with a central stylet and two accessory stylet pouches, is well developed (according to Coe 1943) or rarely strongly developed (after Gibson 1982) and the rhynchocoel is as long as the body, or nearly so. The excretory system is short, anterior in position, and has one or two lateral pores. The intestinal cecum, with or without short anterior branches, and intestine have shallow unbranched lateral diverticulae. In most species, sexes are separate and gonads alternate between the diverticulae.

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Aspects of the Biology of *Pseudocarcinonemertes homari* and Its Association with the American Lobster, *Homarus americanus*

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Aiken, D. E., S. L. Waddy, and L. S. Uhazy. 1985. Aspects of the biology of *Pseudocarcinonemertes homari* and its association with the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 351–356.

Pseudocarcinonemertes homari can reproduce on and destroy the egg mass of both the American (*Homarus americanus*) and the European lobster (*H. gammarus*) but does not appear to be a problem for brachyuran species. The eggs of *P. homari* are subspherical, average 251 × 260 μm, and are contained in individual compartments in a membranous brood sac that is attached to the lobster abdomen or egg mass. An average of 39 eggs occur in a brood sac. Newly hatched larvae are ciliated, lack anterior and posterior tufts, cirri or flagella, and are retained in the brood sac. Larval development is direct, and there is no free-swimming stage. After the larvae break out of the brood sac they join the adults and juveniles on the lobster egg mass. Many lobsters gradually remove infested eggs, but on those that do not, the nemertean population can increase to more than 14 000 individuals. After the lobster eggs are destroyed, the nemerteans disperse. Some form mucoid aggregations at protected sites on the exoskeleton; others move to the branchial chamber and gills or transfer to other lobsters. Reproduction occurs almost exclusively on the lobster egg mass, but *P. homari* appears capable of reproducing on lobster gills if denied access to lobster eggs for extended periods.

Pseudocarcinonemertes homari pond ses œufs sur ceux du homard américain (*Homarus americanus*) et du homard européen (*H. gammarus*) et peut les détruire, mais il ne semble pas poser de problème pour les brachyoures. Les œufs de *P. homari* sont subsphériques et mesurent en moyenne 251 × 260 μm ; ils sont logés dans les compartiments individuels d'un sac membraneux qui s'attache à l'abdomen du homard ou à ses œufs. Un sac contient en moyenne 39 œufs. À l'éclosion, les larves sont ciliées mais ne portent ni cirres, ni flagelles, ni touffe antérieure ou postérieure ; elles demeurent dans le sac. Leur développement est direct et ne comporte pas de stade de nage libre. Après avoir rompu le sac, elles rejoignent les juvéniles et les adultes sur les œufs du homard-hôte. De nombreux homards enlèvent les œufs infestés, mais chez ceux qui ne le font pas, on peut trouver plus de 14 000 némertiens. Lorsque les œufs du homard sont détruits, les parasites se dispersent. Certains forment des aggrégats mucilagineux dans les parties peu exposées de la carapace de l'hôte, d'autres vont dans les branchies et la chambre branchiale ou sur un autre homard. *P. homari* pond presque toujours ses œufs sur ceux d'un homard, mais il semble qu'il puisse les déposer dans les branchies s'il ne peut atteindre la ponte de l'hôte pendant une période prolongée.

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In 1978, adults and juveniles of an unknown nemertean were found among dead and damaged eggs on an American lobster (*Homarus americanus*) from the Bay of Fundy (Aiken et al. 1983). This nemertean was described as *Pseudocarcinonemertes homari* sp. nov. (Fleming and Gibson 1981) and placed in the hoplonemertean family Carcinonemertidae, an assignment questioned by Uhazy et al. (1985).

The literature contains no indication that *P. homari* was associated with the American lobster prior to its discovery by S. L. Waddy in 1978. None of the early reports by investigators who worked with ovigerous American lobsters mention the nemertean (e.g. Herrick 1909; Perkins 1971; Saila et al. 1969; Squires 1970), nor was it reported from surveys of parasites, symbionts, and fouling organisms on lobsters from the Gulf of St. Lawrence (Boghen 1978; Montreuil 1954), the Gulf of Maine (Uzmann 1970), or southern New England (Dexter 1955).

Heavy mortality of lobster eggs was known to occur in the presence of *P. homari* (Aiken et al. 1983), but the cause of mortality was not positively established until lobster vitellin was identified in the gut of *P. homari*, confirming that this nemertean feeds on the eggs of the American lobster (Waddy and Aiken 1985).

The relationship between *P. homari* and the American lobster is similar to that of *Carcinonemertes errans* and the Dungeness crab (Wickham 1978), and *C. errans* has been said to destroy more than 50% of eggs produced by the Dungeness crab in central California waters (Wickham 1979a, 1980). Because of

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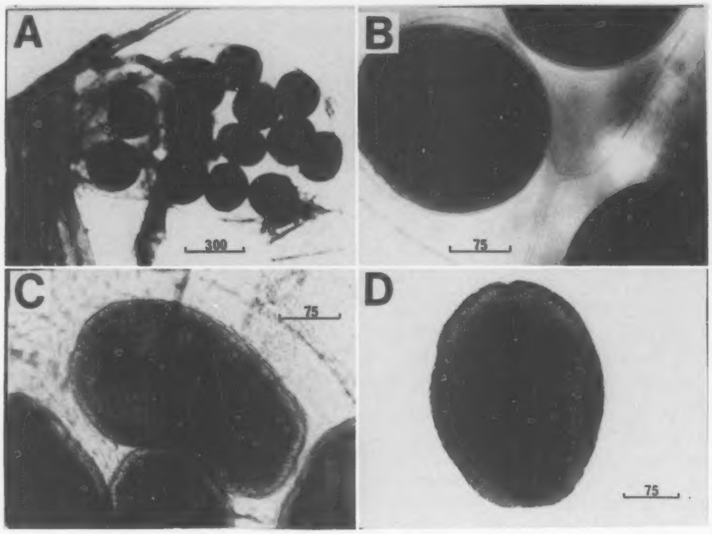

FIG. 1. Brood sacs, eggs, and larvae of *P. homari*. (A) Membranous brood sac attached to nonplumose seta of lobster; (B) eggs in individual gelatinous compartments of brood sac; (C) larva in brood sac with degenerated individual compartments; (D) newly hatched ciliated larva. Scale lines in μm.

the commercial importance of the lobster fishery in the western North Atlantic, studies were initiated on the biology and systematics of the nemertean, its seasonal and geographic variation, and its feeding habits. Several of these aspects are addressed in companion papers (Brattey et al. 1985; Uhazy et al. 1985; Waddy and Aiken 1985). In this report we describe what little is known about the biology of *P. homari* and its relationship to the American lobster. The information is fragmentary, but the objective is to synthesize existing knowledge and highlight areas where additional work is required.

Methods

Lobsters were captured with otter trawl and commercial lobster trap in Passamaquoddy Bay and the Bay of Fundy and held in the lobster culture facility at the Biological Station, St. Andrews, N.B., in broodstock tanks routinely used for the spawning and incubation of eggs for the lobster culture facility. Water in these tanks is maintained at local seawater temperatures, which range from 0 to 14°C, depending on season.

Progress of infestations was monitored by periodic examination of infested lobsters. Systematic samples were conducted in January, April, July, and September, and a photographic record was maintained on individual females. Ad hoc observations were made when conditions warranted.

Live nemerteans were maintained in stacking dishes containing seawater at 4°C. For measurements or examination as live wet mounts they were either anesthetized with 1 mL amyl alcohol/100 mL seawater or slowed by coverslip pressure.

Observations

Early Development

The subspherical eggs of *P. homari* average 251 × 260 μm (25 eggs measured) and are contained in a gelatinous compartment (Fig. 1B) in a membranous brood sac (Fig. 1A) that may be attached to the nonplumose setae, the funiculi of lobster eggs, the membranes of damaged lobster eggs, or the setal fringe of the abdominal pleura. Egg counts on 10 brood sacs revealed a mean of 39 and a range of 30–47 eggs.

Embryological development is different from that reported for other species of *Carcinonemertes* (Humes 1942; Wickham 1980; Stricker and Reed 1981). Cleavage was not studied but the spiral determinate type is characteristic of most nemerteans (Gibson 1972). Larval development is direct, with no free-swimming stage after hatching. Newly hatched larvae are ciliated, lack anterior and posterior tufts, cirri, or flagella, and are retained in the brood sac. The partitions of the individual compartments eventually degenerate (Fig. 1C) and allow the immature nemerteans to move freely within the brood sac, from which they eventually break free (Fig. 1D) to join the adults on the lobster egg mass.

Inpact on Lobster Eggs

The lobster egg mass can become infested at any time during the 10–11 mo from extrusion to hatching, but the number of nemerteans that ultimately develop on the egg mass appears to depend on the developmental stage of the nemerteans that reach the lobster, the degree of lobster egg development at the time of infestation, and the response of the lobster to the infestation. If infestation occurs shortly after the lobster eggs are extruded, there is more time and vitellin available for nemertean development. If gravid female *P. homari* infest the egg mass, the second generation will be produced much sooner than if juvenile or immature nemerteans are involved. Under ideal conditions a so-called "massive" infestation can develop in which the entire egg mass becomes a biological stew consisting of empty egg cases, nemertean brood sacs, larvae, juveniles, and adults, plus assorted epibionts. In one case more than 14 000 individual *P. homari* were removed from a single egg mass (Brattey et al. 1985; Fig. 2). The minimum number of *P. homari* required to induce a destructive infestation has not been determined, but in

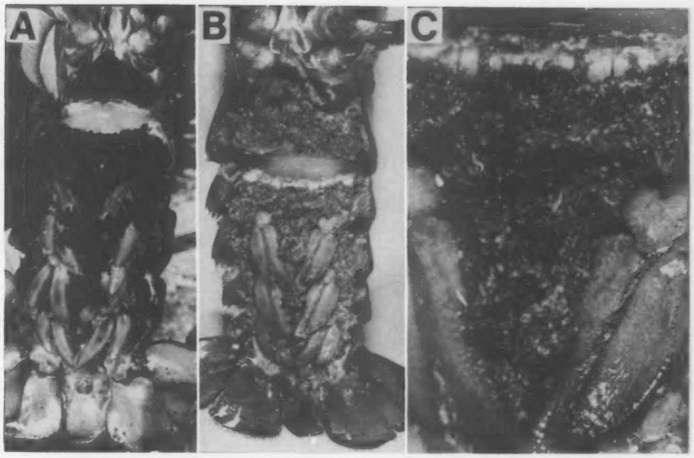

FIG. 2. Massive infestation of a lobster egg mass by the nemertean *P. homari*. (A) Normal egg mass, free of nemerteans; (B) egg mass heavily infested with *P. homari* (more than 14 000 individuals counted); (C) close view of B, showing all stages of nemertean development plus numerous empty lobster egg membranes.

the laboratory, massive infestations have developed from a small number of nemerteans accidentally transferred on the hands of maintenance personnel.

If *P. homari* colonize the egg mass after lobster embryonic development is well advanced, there is less time available for nemertean development and less vitellin available to nurture those that do develop. A lobster egg mass infested at an advanced stage of development will usually hatch some lobster larvae unless the eggs are also fouled by fungal or microbial epibionts (a common occurrence in this and other nemertean species; see Wickham 1979b). A profusion of epibionts can delay or prevent hatching, with or without the presence of *P. homari*.

Field samples indicate that massive infestations are relatively uncommon and that most infestations consist of a relatively small number of nemerteans (Brattey et al. 1985). From laboratory observations, we suspect this is because the majority of females respond to nemerteans by actively removing infested eggs with their chelate pereiopods. Nemerteans, nemertean egg capsules, lobster eggs, and lobster egg membranes are carefully cleaned from the pleopods, and on casual inspection a cleaned female looks like a naturally barren female. Figure 3 shows this gradual removal of an infested egg mass by a "cleaner" compared with the unrestrained nemertean proliferation that occurs on a "noncleaner." Although cleaning activity would appear to be more effective in limiting the number of *P. homari* that result from an infestation, the impact of infestation is the same in each case: destruction of the lobster egg mass.

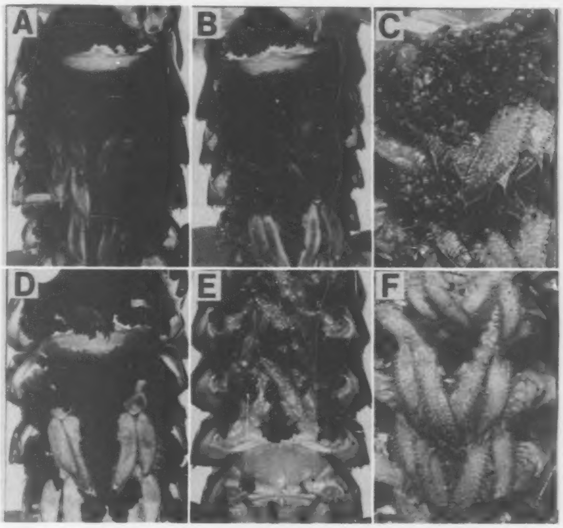

FIG. 3. Effect of lobster cleaning activity on development of *P. homari* on the lobster egg mass from January through July. (A–C) Development of *P. homari* on a "noncleaner" lobster lightly infested in January (A), moderately infested in April (B), and heavily infested in July (C). In the latter case, approximately half of the lobster eggs have been destroyed and the brood chamber is a mass of empty egg cases, dead eggs, nemertean brood sacs, and juvenile and adult nemerteans. (D–F) Development on a "cleaner" lobster, also lightly infested in January (D). By April (E), most of the eggs have been removed and the infestation is still light. By July (F), there are no eggs left and no overt signs of nemertean infestation.

Dispersal

In the laboratory, *P. homari* that are not removed by the lobster will increase in numbers until the lobster embryos either hatch or are destroyed. Either way, diminishing food suppy eventually causes the nemerteans to leave the egg mass. Some remain on the lobster, others leave. In a culture facility, those that leave can be seen in the water column or moving over the floor and walls of tanks. If they remain on the lobster or move to a barren female or male, they either settle in the gills and branchial chamber or form mucoid aggregations on the arthrodial membranes and other protected sites on the exoskeleton (Fig. 4). *Carcinonemertes* apparently do likewise on crabs (Overstreet 1983). The purpose of these aggregations is not known, but recent work by Roe et al. (1981) and Crowe et al. (1982) on *C. errans* indicates that primary amines can pass through the arthrodial membranes from the crab to the surround-

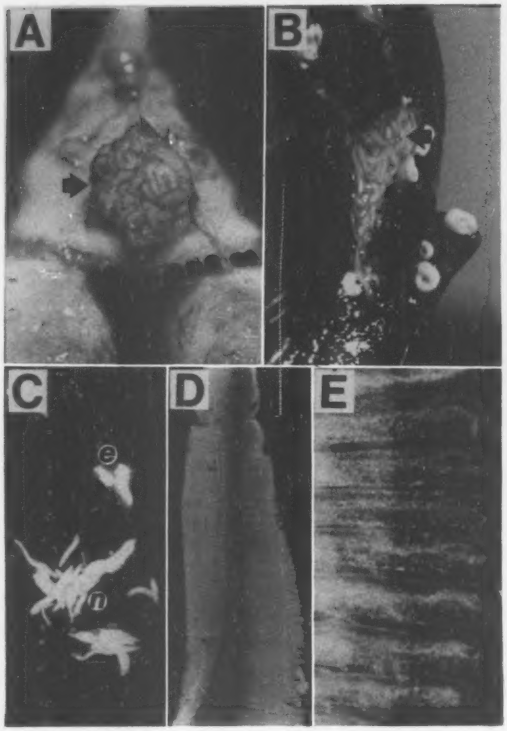

FIG. 4. Sites occupied by *P. homari* after dispersal from the lobster egg mass. Aggregations are seen on sternal plates behind the mandibles (A) and membranes of cheliped joints (B). (C) Nemerteans (n) and nemertean egg sacs (e) on the glass of an aquarium tank after lobster eggs have been destroyed; (D) podobranch of a female that was continuously infested for almost 2 yr. These gill filaments show no sign of infestation or damage (E).

ing seawater, and juvenile *C. errans* are able to absorb these amino acids from the seawater. Because of the similarities in behavior of *C. errans* and *P. homari*, this possibility would be worth investigating in the latter species.

Impact on Males and Barren Female Lobsters

Fleming and Gibson (1981) suggested that the ultimate destination of dispersed nemerteans is the branchial chamber and the gill filaments, but the extensive samples of Brattey et al. (1982) show no clear preference for the branchial region over any other protected site on the body. We have found large numbers of *P. homari* among the gill filaments of some lobsters, but seldom to the exclusion of other protected sites on the exoskeleton. However, the mucoid aggregations that occur elsewhere on the exoskeleton have not been seen on the gills or in the branchial region (cf. Gibson 1972 for *Carcinonemertes*).

We have found undamaged gill tissue on three females that were continuously infested with *P. homari* for almost 2 yr (Fig. 4), but one 11.5-kg male held in isolation for 2 yr in our system died from extensive gill damage, and the gills were heavily infested with *P. homari* (Fig. 5). This infestation contained all stages of nemertean development, brood sacs, larvae, juveniles, and gravid adults, and appeared to be self-sustaining. Microbial epibionts were present but insignificant, given the extent of damage, and *P. homari* was the only organism present in appreciable numbers.

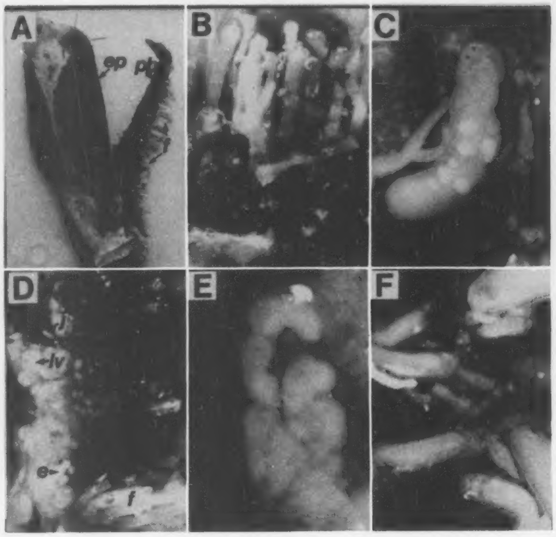

FIG. 5. Damage to gills of a male lobster infested with large numbers of *P. homari*. (A) Gill of 11.5-kg male, showing melanization of gill separator (ep) and podobranch (pb), and extensive destruction of gill filaments (f); (B) close view of podobranch showing destruction of filaments; (C) mature female *P. homari* on podobranch; (D) eggs (e), larvae (lv), and small juvenile (j) *P. homari* on podobranch; (E) larvae still contained in brood sac; (F) variety of sizes of *P. homari* present on the podobranch.

Host Specificity

In addition to the American lobster, *P. homari* has proved to be persistant and destructive on a female European lobster (*Homarus gammarus*) held in the culture facility. In spite of repeated attempts to eliminate the nemertean and isolate the female from contact with the nemertean, this lobster has lost two broods to nemerteans in 3 yr.

We have exposed ovigerous rock crabs (*Cancer irroratus*) to *P. homari* in tanks containing infested lobsters. Although the occasional nemertean was observed on the *Cancer* crabs and egg masses, there was no evidence of egg destruction or nemertean reproduction. These results corroborate the work of Brattey et al. (1982), who examined five species of crabs in Atlantic waters and concluded that *P. homari* is specific to lobsters.

Discussion

The biological similarities between *P. homari* and *C. errans* have been noted, but the following information, summarized from Overstreet (1983) for *Carcinonemertes carcinophila* and similar species, make it obvious that *P. homari* shares many of the biological and behavioral peculiarities of this genus.

Many of the *Carcinonemertes* species, like *P. homari*, are also narrow in their selection of host species and show a predilection for the gills and branchial chamber. Several also form mucoid aggregations on the host. *Pseudocarcinonemertes homari* aggregate at protected sites such as the sternal plates and limb joints, similar to *Carcinonemertes epialti*. Both species can break out of an aggregation on one host and form new aggregations on a different host. After the crab eggs hatch or are destroyed, adult *C. carinophila* stop feeding, move to the gill lamellae, lose some of their adult characteristics, and await another clutch of crab eggs. About the most significant behavioral deviation displayed by *P. homari* is its preference for a macruran rather than a brachyuran host.

Miller and Fleming (1983) reported that infested lobsters held up to 5 mo in a recirculating water system suffered extensive damage to gill filaments from the feeding activity of *P. homari*, and this contributed to secondary invasion by pathogenic fungi which "may ultimately cause the death of the lobster. ..." Although we have seen extensive gill damage caused by *P. homari*, we have not seen the extensive secondary invasion by facultative pathogenic fungi described by Miller and Fleming (1983). It should be noted that the black–brown areas they described on the gill filaments are also common on gill filaments of lobsters from the Gulf of St. Lawrence, where the incidence of *P. homari* is low. We suspect there are multiple causes of such lesions.

We have seen infested barren lobsters with no nemerteans on the gills, infested barren lobsters with nemerteans on the gills but no apparent damage, even after prolonged infestation, and an infested barren lobster with nemerteans on the gills and extensive gill damage. Overstreet (1983) noted that destruction of gill tissue was rare, even in species that routinely infest crab gills in large numbers, and this would seem to be the case with *P. homari* as well. This raises a basic question: under what conditions does *P. homari* feed extensively on the gills of lobsters?

The one instance of extensive gill damage we observed occurred in a male isolated physically and by water suppy from other lobsters in the facility. We do not know how long this lobster was infested with *P. homari*, but it could have been as much as 2 yr. *Pseudocarcinonemertes homari*, like many nemerteans, can survive for extended periods without food, but it is possible that the nemerteans on this particular lobster were denied access to an egg mass for longer than they are capable of surviving without food. In such a situation the nemertean may begin feeding on lobster gills. The photographs in Fig. 5 show that *P. homari* was also reproducing on the gills of the lobster, a phenomenon not reported for *Carcinonemertes* (Gibson 1972). Since starved nemerteans tend not to reproduce (Bierne 1983), this is a further indication that the nemerteans were deriving nourishment from the gill tissue. However, considerably fewer eggs were seen in the ovaries of gravid females on the gill tissue than in comparable females on a lobster egg mass, and the membranous egg sacs attached to the lobster gills contained only 4–8 eggs, compared with the 30–47 found in egg sacs removed from a lobster egg mass. The nemertean ovary is capable of producing 20–50 eggs, but competition and resorption may reduce this to 4–10 eggs by the time they are deposited (Bierne 1983). Furthermore, gravid *P. homari* on an egg mass tend to develop their ovaries to capacity (a gonad index of roughly 90%), whereas those seen on gill tissue had oocytes developing in only a few of their ovaries. It would therefore appear that lobster eggs provide maximum nourishment (and reproductive potential) for *P. homari* but gill tissue does not, and lobster gill tissue may be utilized as emergency nourishment for *P. homari* denied access to lobster eggs for long periods. In the wild the ready accessibility of ovigerous females in most areas would make it unnecessary for *P. homari* to feed on gill tissue, thus explaining the absence of gill damage among lobsters examined in field samples (Brattey et al. 1985).

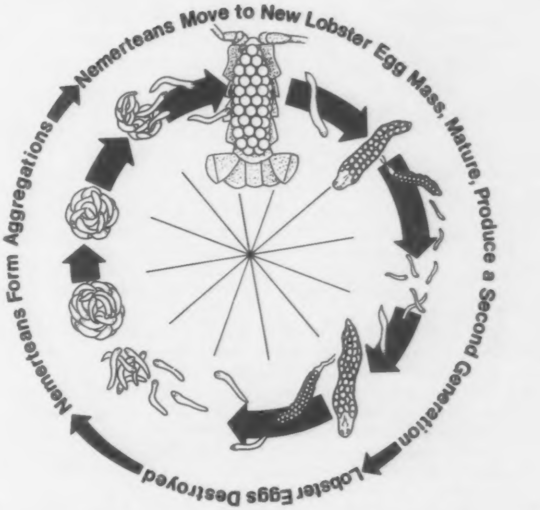
Nemerteans Move to New Lobster Egg Mass, Mature, Produce a Second Generation
Lobster Eggs Destroyed
Nemerteans Form Aggregations

FIG. 6. Generalized 12-mo cycle of interaction between *P. homari* and the American lobster. There are several variations, mostly dependent upon the degree of lobster egg development at the time of infestation and the response of the lobster to the infestation.

One of the important observations in this study is the "cleaning" activity by a significant percentage (possibly the majority) of ovigerous lobsters once *P. homari* begins to reproduce on their egg mass. Removal of infested eggs along with associated nemerteans clearly limits the number of nemerteans that can be produced on an egg mass. It does not limit the damage to the egg mass, since all eggs are ultimately destroyed. However, cleaning activity may mask the damage done by *P. homari* by increasing the apparent number of lightly infested ovigerous females and decreasing the number of heavily infested ovigerous females seen in field samples.

There have been no detailed or systematic studies of the life history of *P. homari* on American lobsters but it is possible to draw on the observations of different investigators to construct an annual cycle of events. These are summarized in Fig. 6. Although this represents a typical series of events, the variations are many. For example, Fig. 6 shows the lobster egg mass being infested by juveniles from aggregations formed on the exoskeleton of the same or a different female lobster. Evidence suggests that females may also be infested by mature nemerteans displaced from a lobster egg mass that has been destroyed (or hatched). Although reproduction is seasonal in most nemerteans (Bierne 1983), only slight seasonal trends can be detected in field samples of *P. homari* (Brattey et al. 1985).

In spite of the parallels between *P. homari* and the various species of *Carcinonemertes*, we still know very little about the basic biology of this nemertean. We have no firm insight on the origin of the organism as a consumer of lobster egg vitellin (or gill tissue, for that matter), and no way of knowing whether natural controls limit its population in relation to the lobster or its distribution throughout the range of the lobster. We do not know, for example, whether the current range is stable or expanding, and what factors determine its extent. We lack information on such basic questions as the life span of the average *P. homari*, the number of reproductive cycles a female may go through in her life span, the effect of temperature on the survival and development of the animal, whether eggs and small juveniles displaced from an egg mass can survive, and whether some female lobsters are resistant to infection. Finally, we have no way of controlling this organism on lobsters, either in the wild or in captivity. The implications of this problem to the lobster industry are considerable.

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Immunofluorescent Localization of American Lobster Egg Yolk Protein in the Alimentary Tract of the Nemertean *Pseudocarcinonemertes homari*

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A direct immunofluorescent antibody test revealed the presence of American lobster, *Homarus americanus*, egg yolk protein in the alimentary tract of the nemertean *Pseudocarcinonemertes homari*. Nemerteans that had been in contact with lobster eggs demonstrated strong fluorescence in the area of the sections identified as the intestinal diverticula, while those nemerteans that had not been in contact with lobster eggs did not. This provides the first direct evidence that *P. homari* actually consumes lobster egg yolk.

Par un test d'immunofluorescence direct, nous avons détecté une protéine du vitellus des œufs de homard américain, *Homarus americanus*, dans le tube digestif du némertien *Pseudocarcinonemertes homari*. Nous avons mesuré une forte fluorescence dans le diverticule intestinale de némertiens placés en contact avec des œufs de homard, phénomène qui ne s'est pas manifesté chez les sujets qui n'étaient pas en contact avec des œufs. C'est là la première preuve directe que *P. homari* mange le vitellus des œufs de homard.

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A new species of nemertean, *Pseudocarcinonemertes homari*, has been found on the egg mass of the American lobster, *Homarus americanus* (Aiken et al. 1980, 1983, 1985; Fleming and Gibson 1981; Uhazy et al. 1985). Although this nemertean is associated with egg loss or extensive destruction of the egg mass (Aiken et al. 1980, 1983, 1985), conclusive evidence that the nemertean actually feeds on the eggs or is in any way directly responsible for egg destruction has been difficult to obtain. Nemertean infestations tend to support a variety of bacterial, fungal, and protozoal organisms which could cause the death or loss of the lobster eggs.

On the basis of nemertean behavior and egg mortality over time, Wickham (1978, 1979a, 1979b, 1980) concluded that a similar nemertean, *Carcinonemertes errans*, was feeding on the eggs of the Dungeness crab (*Cancer magister*) and estimated that over a 5-yr period 55% of eggs produced by the central California Dungeness crab population were destroyed by this nemertean. As noted previously (Aiken et al. 1980, 1983), the nemerteans associated with the Dungeness crab and the American lobster, though taxonomically distinct, have a similar biology in relation to their host (Aiken et al. 1985). Both move to the egg mass after oviposition, mature, lay their own eggs among those of the host, appear to feed on the eggs of the host, and are capable of causing extensive egg loss and contributing to the development of associated microbial epibionts. After the lobster eggs hatch or are destroyed, the nemerteans infesting the lobster egg mass leave the ventral abdomen (brood chamber) of the host and form communal aggregations at protected locations on the abdomen, thorax, and appendages where they can remain for many months in a dormant state (Aiken et al. 1983, 1985).

Direct evidence that nemerteans, infesting the egg mass of either crabs or lobsters, are actually feeding on the eggs has been difficult to obtain. Wickham (1978) described the movements necessary for *C. errans* to bring its proboscis stylet into contact with the egg membrane, and was of the opinion (Wickham 1979a, 1979b) that they were consuming the egg yolk, but was unable to obtain conclusive evidence of this. There seems little question the nemerteans are associated with egg loss and destruction, but egg destruction contributes to the growth of epibionts, which could themselves cause egg mortality or serve as food for the juvenile and adult nemerteans. The basic question is whether the nemerteans causes egg mortality by consuming the egg yolk itself or by simply puncturing the egg membrane and releasing the yolk, thereby creating an environment for the growth of other organisms that might be the principal source of nutrients for the nemertean. Therefore, the only conclusive evidence of yolk consumption by the nemertean will be the demonstration of lobster egg yolk in the alimentary tract of the nemertean.

Serological techniques have been widely used to identify prey proteins in a predator (for review, Boreham and Ohiagi 1978), and immunofluorescent techniques can be easily used to localize a specific protein in tissues. Lobster eggs are composed of proteins unique to the species, so antibodies raised against these proteins can be used immunologically to reveal the presence of lobster egg yolk proteins in a suspected predator. This paper describes the use of a serological precipitation test and an immunofluorescent test to establish the presence of lobster yolk proteins in the nemertean predator–parasite found in association with those eggs.

Methods

Lobster ovaries determined to be stage 4 according to the system of Aiken and Waddy (1980) were removed from

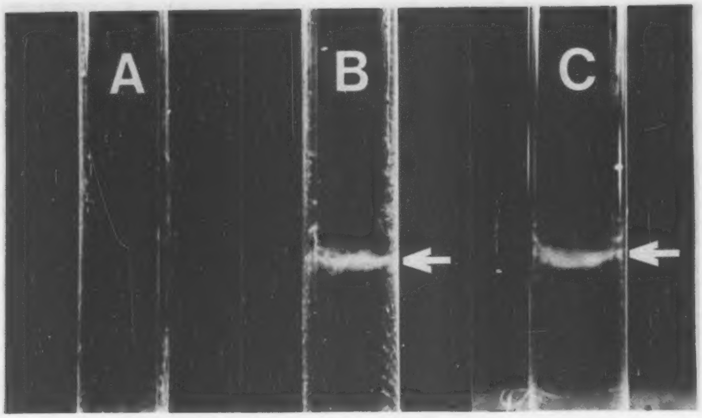

FIG. 1. Serological precipitin tests using anti-lobster serum. (A) Homogenized nemertean eggs; (B) homogenized lobster eggs; (C) homogenized whole nemerteans removed from a lobster egg mass. Precipitation bands (arrows) indicate positive antigen–antibody reaction (i.e. presence of lobster yolk proteins).

nemertean-free lobsters, and the yolk proteins were extracted according to the method of Wallace et al. (1967). Rabbit anti-lobster serum against these yolk proteins was produced by Antibodies Inc., Davis, California, according to their standard 3-wk protocol.

More than 100 nemerteans and nemertean eggs were obtained from the egg mass of two ovigerous lobsters from the Bay of Fundy. They were homogenized separately in an ultrasonic cell disrupter in a minimal amount of 0.5 mol NaCl/L – 5 mmol EDTA/L and centrifuged at 15 000 rpm for 20 min. The supernatants were used in an interfacial precipitation test (Kwapinski 1965) run for 3 h at room temperature. NaCl–EDTA was used as a blank control, and homogenized lobster eggs from an uninfested female lobster were used as a control antigen.

The globulin fraction of the anti-lobster serum was separated by precipitation with ammonium sulfate (Goldman 1968) and then labeled with fluorescein isothiocyanate (FITC) (Sigma) by a method adapted from Clark and Shephard (Goldman 1968). Unreacted FITC was removed by dialysis. Two groups of nemerteans were tested: nemerteans removed from lobster eggs and starved for 4 d before sectioning, and nemerteans from this starved group that were allowed contact with live lobster eggs for 24 h before sectioning. Four nemerteans from each group were sectioned. Frozen sections of live, unfixed tissue were cut at 20 μm and post-fixed in 95% EtOH. Using a direct staining technique (Goldman 1968), reactions were carried out at room temperature for 60 min. Consecutive sections were examined for autofluorescence, nonspecific staining and fluorescence after incubation. Control sections were stained with nonlabeled antibody and with FITC not conjugated with antibody.

Results and Discussion

The initial interfacial precipitation test was used to determine if there was any association between lobster egg yolk and adult nemerteans. No precipitation band was obtained with either the blank control (NaCl–EDTA) or homogenized nemertean eggs (Fig. 1A), indicating no immunological identity between nemertean egg yolk and lobster egg yolk. A positive precipitation band (Fig. 1B) was obtained using lobster eggs and nemerteans obtained directly from the lobster egg mass (Fig. 1C). Ideally the gut should be dissected from the nemertean and tested in isolation, but this was technically very difficult with this small nemertean, so homogenized whole nemerteans were used. Although these results demonstrated the presence of lobster egg yolk in the nemertean sample, there was a possibility

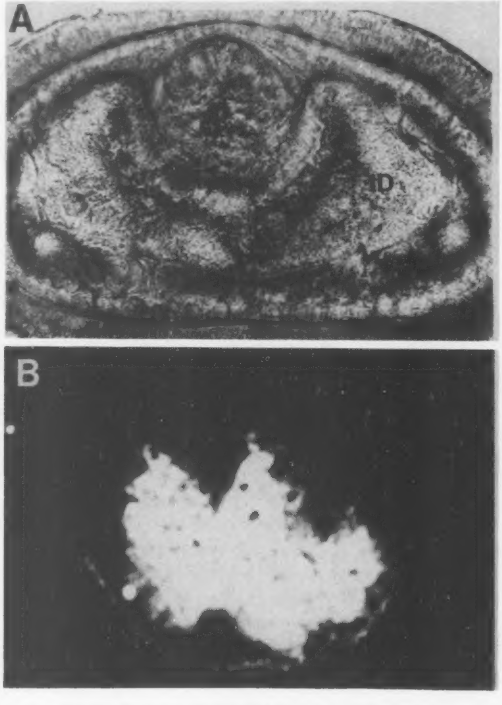

FIG. 2. Immunofluorescent test using anti-lobster serum. (A) Cross section of unstained nemertean indicating the butterfly-shaped intestinal diverticula (ID) (photograph courtesy of L. S. Uhazy); (B) cross section of nemertean stained with FITC-labeled antibody revealing antibody reaction in the area of the intestinal diverticula.

the antigen was reacting to lobster yolk protein on the external surfaces of the nemertean instead of in the gut. To identify the specific site of reaction, anti-lobster serum labeled with FITC was used. Transverse sections of whole adult nemerteans starved for 4 d did not react with the labeled antibody, whereas those same starved nemerteans allowed to feed on live lobster eggs for 24 h prior to sectioning and staining with fluorescent-labeled egg-yolk antibody did react. Lobster yolk protein was demonstrated in the area of the sections identified as the intestinal diverticula (Fig. 2B). Transverse sections of an unlabeled nemertean show butterfly-shaped intestinal diverticula in the central portion of the nemertean (Fig. 2A). This same pattern is apparent in the FITC–antibody stained sections (Fig. 2B), indicating lobster yolk protein is concentrated in the gut and intestinal diverticula. No fluorescence was detected in sections incubated in nonlabeled antibody nor in sections stained with unconjugated FITC.

These results are interpreted as the first conclusive evidence that the nemertean found in association with the egg mass of wild American lobsters is feeding directly on the contents of the eggs.

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Geographic Distribution and Seasonal Occurrence of the Nemertean *Pseudocarcinonemertes homari* on the American Lobster, *Homarus americanus*

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Examination of 1041 trap-caught lobsters from the Bay of Fundy, Grand Manan, Browns and German Banks, south and east Nova Scotia, and Northumberland Strait indicated that *Pseudocarcinonemertes homari* occurs on American lobsters, *Homarus americanus*, throughout Canadian Maritime waters. Male lobsters were rarely infected and ovigerous females generally had a higher prevalence (percentage infected) and mean intensity of infection (number of nemerteans per infected lobster) than nonovigerous females. Sexually immature nemerteans were found on male and nonovigerous female lobsters, but all *P. homari* life history stages including brood sacs occurred on ovigerous lobsters. No seasonal trends were evident on ovigerous lobsters caught near Grand Manan; prevalence was consistently high (60–93%) and mean intensity ± SE was variable (15 ± 4.0 to 86 ± 63.1). The nemertean developed to maturity on ovigerous lobsters, reproduced on the host egg masses throughout the year, and appeared to produce three generations during a lobster egg incubation period. When lobsters completed egg incubation, nemertean reproduction ceased and some nemerteans either died, left the lobster, or perhaps were shed at molting. Prevalence and mean intensity increased with the size of ovigerous lobsters, and the distribution of nemerteans among ovigerous lobsters was highly aggregated. Ovigerous lobsters infected with >200 nemerteans had extensively damaged egg masses, but were rarely encountered (5 of 291). The impact of *P. homari* on the egg mortality of wild populations of *H. americanus* is unknown.

L'examen de 1041 homards capturés au casier dans la Baie de Fundy, à Grand Manan, sur les bancs Browns et German, au sud et à l'est de la Nouvelle-Écosse et dans le détroit de Northumberland a montré que *Pseudocarcinonemertes homari* infestait des homards américains, *Homarus americanus*, dans toutes les eaux des provinces maritimes. Les homards mâles étaient rarement infestés et les femelles œuvées présentaient généralement une prévalence (pourcentage de sujets infestés) et une intensité moyenne d'infestation (nombre de némertiens par sujet) plus élevées que les femelles non œuvées. Des némertiens sexuellement immatures ont été trouvés dans des mâles et des femelles non-œuvées, mais des *P. homari* de tous les stades de développement, y compris celui à sac origène, ont été observés chez des femelles œuvées. Aucune tendance saisonnière n'était évidente. Chez les femelles œuvées capturées près de Grand Manan, la prévalence était constamment élevée (60 à 93 %) et l'intensité moyenne ± E-T était variable (15 ± 4,0 à 86 ± 63,1). Les némertiens se développaient jusqu'à maturité sur les femelles œuvées et se reproduisaient sur les masses d'œufs de l'hôte tout au long de l'année ; ils semblaient produire trois générations au cours de la période d'incubation des œufs. Une fois l'incubation des œufs terminée, les némertiens cessaient de se reproduire et certains mouraient, quittaient le homard ou, peut-être, étaient rejetés lors de la mue. La prévalence et l'intensité moyenne augmentaient avec la taille des femelles œuvées et la répartition des némertiens chez ces femelles était fortement regroupée. Les femelles œuvées infestées par plus de 200 némertiens présentaient des masses d'œufs fortement endommagées, mais ces femelles étaient rare (5 sur 291). L'incidence de *P. homari* sur la mortalité des œufs des populations sauvages de *H. americanus* demeure inconnue.

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Pseudocarcinonemertes homari Fleming and Gibson 1981 is an ectosymbiotic nemertean found on the exoskeleton, branchial chambers, and egg masses of American lobsters, *Homarus americanus*. Considerable interest in *P. homari* has arisen among biologists, because its presence is often associated with extensive destruction of lobster egg masses (Fleming and Gibson 1981; Aiken et al. 1983). Observation of infected lobsters maintained in aquaria suggests that destruction of lobster eggs results from (1) nemerteans feeding on the eggs, (2) secondary fouling by microbial epibionts, and (3) lobsters picking off their eggs in response to the nemertean infection (Aiken et al. 1985; Waddy and Aiken 1985). Substantial nemertean-induced egg losses have been observed among populations of other economically important species of decapod crustacean (Wickham 1979a, 1979b). Consequently, there are concerns about the possibility of *P. homari* infestation lowering the reproductive potential of commercially important lobster populations.

Previous surveys of parasites and fouling organisms of the American lobster (Montreuil 1954; Dexter 1955; Uzmann 1970; Boghen 1978) did not find *P. homari* and nothing was known about the ecology of the nemertean. However, since the discovery of the nemertean on *H. americanus* (Aiken et al. 1983), we undertook to investigate the geographic distribution of *P. homari* in Canadian Maritime waters and to provide some indication of the prevalence and intensity of infection of the nemertean on commercially caught male and female lobsters in each area surveyed. In this paper, we present the results of this survey. Initial findings from the geographic survey had indicated that a large proportion of the lobsters from Grand Manan were infected with *P. homari*. Consequently, we also present data on seasonal changes in the occurrence, life history, and distribution of *P. homari* on mature female lobsters caught in traps near North Head, Grand Manan, during 1980–82.

Materials and Methods

A total of 1041 commercially caught lobsters were obtained at depths of 6–250 m at five areas in Canadian Maritime waters (Fig. 1). On removal from traps, lobsters were immediately placed individually into polyethylene bags, labeled with the date, depth, and location of capture, placed in an insulated cooler, and within 6 h frozen at −20°C for storage. After thawing, carapace length (CL), in millimetres, was measured using a vernier caliper from the base of the eye socket to the posterior margin of the carapace parallel to the mid-dorsal line.

Thawed lobsters and bags were washed thoroughly with fresh water. Washings were collected, poured through sieves of 1-mm and 80-μm mesh, resuspended in fresh water, and examined for nemerteans and nemertean brood sacs with a stereo microscope. The body surface of each lobster was examined after washing. Eggs and pleopods of ovigerous lobsters, and the gills of all lobsters, were removed and shaken in a vessel containing fresh water and the washings resuspended in fresh water, sieved, and examined. The inner lining of the lobster carapace, excised gills, and egg masses were also examined after washing. For the geographic survey, all nemertean worms were counted and preserved in 10% formalin or a 1:9 solution of 10% glycerol in 70% ethanol. The exceptionally large numbers of nemerteans on two lobsters were estimated volumetrically by calculating the mean number of nemerteans in a series of equal volume subsamples and determining total numbers by multiplication.

The effect of freezing on our ability to distinguish nemerteans was unknown; thus, our method of storage and examination of lobsters was tested; known numbers of live nemerteans at various stages of development were placed in containers with seawater and samples of fresh lobster eggs. These were frozen (−20°C) for >3 wk. Samples were thawed, washed, and sieved by an observer unaware of the original number of nemerteans in each container. Twenty replicates were conducted and they gave a mean recovery of 96.2% (range 92.4–100%). Consequently, our method of storage and examination was assumed to be accurate.

For the seasonal analyses of *P. homari* near North Head, Grand Manan (Fig. 1), only female lobsters were included because male lobsters were rarely infected. When present, lobster eggs were examined and categorized as newly extruded, developing, or close to hatching, according to the degree of development of the lobster embryos. Nemertean worms were counted, but nemertean brood sacs were noted only as present or absent. To determine their stage of maturity, nemerteans were placed in a 1:9 solution of 10% glycerol in 70% ethanol, the ethanol was allowed to evaporate to render the gonads more visible, and gonad diameter was used as an index of nemertean maturity. We used a stereo microscope at ×40 magnification to assign nemerteans to one of three maturity stages: stage I, sexually immature, small (<2 mm in length), whitish, with no gonads visable; stage II, partly developed females and partly developed and sexually mature males, usually orange, with small spherical gonads <120 μm in diameter situated between the intestinal diverticulae (see Fleming and Gibson 1981); stage III, gravid females, bright orange, with conspicuous spherical yellowish ova 120–250 μm in diameter distributed irregularly throughout the body. Nemertean brood sacs were also dissected and examined to determine the extent of larval nemertean development.

Prevalence is defined as the percentage lobsters infected and mean intensity as the mean number of nemerteans per infected lobster (Margolis et al. 1982). For the geographic survey, *G*-tests (Sokal and Rohlf 1969) were used to determine the significance of differences in nemertean prevalence between areas or between male, nonovigerous, and ovigerous female lobsters. Nonparametric one-way ANOVA (Kruskal–Wallis test) was used to determine the significance of geographic differences in mean intensity. The Mann–Whitney U test (Siegel 1956) was used to investigate differences in median intensity between male, nonovigerous, and ovigerous female lobsters. Prevalence and median intensity did not differ significantly ($p > 0.05$) between samples of lobsters collected at locations within the same area; thus, data were combined to represent five general areas for convenience in further analyses. The areas are (1) Bay of Fundy (Chance Harbour, Delap Cove, Alma), (2) Grand Manan (North Head), (3) Browns and German Banks, (4) south and east coast of Nova Scotia (Port Maitland, Port Mouton, Three Fathom Harbour, Fourchu), and (5) Northumberland Strait (Point Sapin, Egmont Bay, Cape Tormentine, Victoria, Beach Point) (Fig. 1). The range of lobster CL and dates when samples were obtained from each area are as follows: Bay of Fundy (70–150 mm CL), April–November 1980 and September 1981; Grand Manan (90–180 mm CL), June 1980 – September 1982; Browns and German Banks (80–170 mm CL), July 1980 – July 1981; south and east coast of Nova Scotia (80–140 mm CL), April 1980 – December 1981; Northumberland Strait (60–140 mm CL), September 1980 – Sepember 1982.

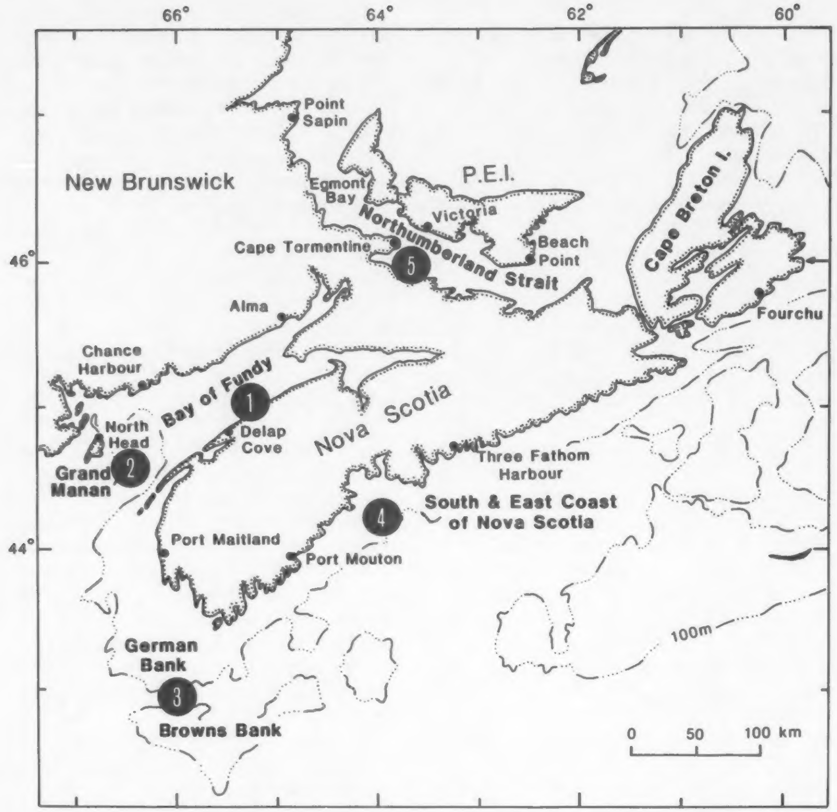
66°
64°
62°
60°
46°
44°
Point Sapin
New Brunswick
P.E.I.
Egmont Bay
Victoria
Northumberland Strait
Beach Point
Cape Tormentine
5
Cape Breton I.
Fourchu
Alma
Chance Harbour
Bay of Fundy
1
North Head
Delap Cove
Nova Scotia
Grand Manan
2
Three Fathom Harbour
South & East Coast of Nova Scotia
4
Port Maitland
Port Mouton
German Bank
3
Browns Bank
100m
0 50 100 km

FIG. 1. Location of the five lobster sampling areas: 1, Bay of Fundy; 2, Grand Manan; 3, Browns and German Banks; 4, south and east coasts of Nova Scotia; 5, Northumberland Strait.

For the seasonal analyses, to investigate differences in prevalence and mean intensity either between monthly samples or between lobster size groups, we used the *G*-test and nonparameric one-way ANOVA (Kruskal–Wallis test), respectively (Sokal and Rohlf 1969).

Results

Geographic Distribution

Pseudocarcinonemertes homari was found on lobsters in all areas and all depths sampled. All nemertean life history stages, from eggs enclosed in gelatinous brood sacs to sexually mature adults, were found on ovigerous lobsters, whereas only immature nemerteans were found on nonovigerous females and males. The nemerteans were found in crevices on the exoskeleton, in the branchial chambers, among the gill filaments, and particularly on the egg masses of ovigerous lobsters. Nemertean brood sacs were found on the pleural setae, pleopods, and egg masses of ovigerous lobsters.

Prevalences of *P. homari* were highest on ovigerous lobsters in all areas, although they ranged widely from 3.6% in Northumberland Strait to 78.7% in Grand Manan (Table 1). On male and nonovigerous females, prevalences were low (≤7.5%), except for nonovigerous females from Grand Manan (30.8%). Caution in interpretation of data should be made, since in some areas sample sizes were small ($N < 25$) although similar differences in prevalence between males, ovigerous, and nonovigerous females were observed for all areas.

TABLE 1. Prevalence of *P. homari* on lobsters from Canadian Maritime waters (sample sizes are in parentheses). Prevalences in same rows not followed by the same letter are significantly different ($p < 0.05$) using the *G*-test (Sokal and Rohlf 1969).

Area	Males	Nonovigerous females	Ovigerous females
Bay of Fundy	2.2 (90) a	2.4 (84) a	36.0 (25) b
Grand Manan	7.5 (106) a	30.8 (107) b	78.7 (291) c
Browns and German Banks	0 (56) a	0 (48) a	16.9 (53) b
South and east Nova Scotia	3.4 (29) a	5.6 (36) a	31.6 (19) b
Northumberland Strait	0 (25) a	0 (16) a	3.6 (56) a

There were significant differences in prevalence among the five areas for nonovigerous females ($p < 0.001$) and for ovigerous females ($p < 0.001$). Nemerteans were generally rare and only occurred on ovigerous lobsters on Browns and German Banks (16.9%) and in Northumberland Strait (3.6%). Highest prevalences for males (7.5%), nonovigerous females (30.8%), and ovigerous females (78.7%) occurred at Grand Manan.

Mean intensities were generally greater for infected ovigerous lobsters (1.0–102.4) than those for nonovigerous females (5.0–14.5) and males (1.5–6.3) (Table 2). Five of 291 ovigerous lobsters from Grand Manan were infected with 266 –

TABLE 2. Mean intensity of *P. homari* on infected lobsters from Canadian Maritime waters (n = number of infected lobsters). Medians in same row not followed by the same letter are significantly different ($p < 0.05$) using the Mann–Whitney U test (Siegel 1956).

Area		Males	Nonovigerous females	Ovigerous females
Bay of Fundy	Mean ± SE	1.5	5.0	13.8±10.2
	Median	1.5 a	5.0 a	5.0 a
	n	2	2	9
Grand Manan	Mean ± SE	6.3±4.9	12.6±4.1	102.4±64.6
	Median	3 a	16 b	48 c
	n	8	33	229
Browns and German Banks	Mean ± SE	0	0	6.1±3.3
	Median	0	0	4.0
	n	0	0	9
South and east coasts of Nova Scotia	Mean ± SE	1.0	14.5	7.8±2.9
	Median	1.0 a	14.5 a	5 a
	n	1	2	5
Northumberland Strait	Mean ± SE	0	0	1.0
	Median	0	0	1.0
	n	0	0	2

14 750 nemerteans and had extensively damaged egg masses. There were significant differences in mean intensity among the five areas for nonovigerous female ($p < 0.001$) (Table 2). Nemerteans were most abundant on ovigerous lobsters from Grand Manan. There were insufficient numbers of infected males and nonovigerous females to compare all areas.

Seasonal Occurrence

Lobster egg incubation period

Although the approximate duration and timing of lobster egg incubation at Grand Manan are known (Aiken and Waddy 1980), precise information was required for this study. Examination of lobster eggs and developing embryos indicated that female lobsters at Grand Manan extrude eggs during August and September, and incubate them for 10–12 mo until they hatch during July–August of the following year (Fig. 2A). A slight overlap of egg incubation periods occurred during August 1982, when two distinct "populations" of ovigerous lobsters were observed, i.e. those with eggs about to hatch and those with newly extruded eggs. Mature female lobsters usually remain nonovigerous for approximately 9–12 mo after an egg incubation cycle is completed (Aiken and Waddy 1980).

Nemertean life history

Ovigerous females — Brood sacs of *P. homari* were found on the pleopods, pleural setae, and egg masses of ovigerous lobsters. They were present at all times of year (Fig. 2B), although prevalence differed significantly between samples ($p < 0.01$, df = 13) and appeared to increase as lobster egg incubation progressed. Brood sacs collected from lobsters during August and September 1982 (i.e. with new egg masses) always contained undeveloped nemertean eggs. However, brood sacs present at other times contained undeveloped nemertean eggs, developing nemertean larvae, or fully developed juvenile nemerteans with eyespots. Empty brood sacs were also observed, suggesting that juvenile nemerteans had already emerged.

Nemerteans were found on the exoskelton, in the branchial chambers, and particularly on the egg masses of ovigerous lobsters throughout the study period (Fig. 2C). Prevalence of infection was consistently high (60–93%) but differed significantly between monthly samples ($p < 0.01$, df = 13). Mean intensity fluctuated from 15 ± 4.0 to 86 ± 63.1 and there was considerable variation in the number of nemerteans recovered from lobsters collected at similar times. No distinct seasonal trends in mean intensity were observed but mean intensities were higher ($p < 0.01$) for November 1980 and February, April, and August 1981 than for the other months (Fig. 2C). Although mean intensity was related to the size of ovigerous lobsters (see last paragraph of Results), size frequency distributions of lobster samples were not significantly different (one-way ANOVA, $p > 0.05$, df = 13). Thus, seasonal differences in mean intensity were not solely due to heterogeneity in the size composition of the lobster samples.

Seasonal changes in *P. homari* population structure on ovigerous lobsters are shown in Fig. 2D. Nemerteans at various stages of maturity (i.e. immature, developing, and gravid) were present at all times, and similar changes in population structure appeared to take place during two consecutive lobster egg incubation periods. Although *P. homari* appeared to reproduce on ovigerous lobsters throughout the year (Fig. 2B), the nemertean population during each incubation period was apparently trivoltine (Fig. 2D). Successive generations of *P. homari* appeared during fall (August–October), winter and early spring (November–April), and late spring and summer (May–August). The first generation comprised nemerteans that colonized ovigerous lobsters soon after eggs masses were extruded, or were present beforehand. They were already mature, or matured, and females deposited brood sacs during August–October. Immature nemerteans, representing the second generation, probably emerged from the brood sacs during October–November, and they developed to maturity by April–May of the following year. The second generation produced brood sacs during April–August. Immature nemerteans, representing a third generation, appeared during May–August. The generations were not distinct and tended to overlap, and there

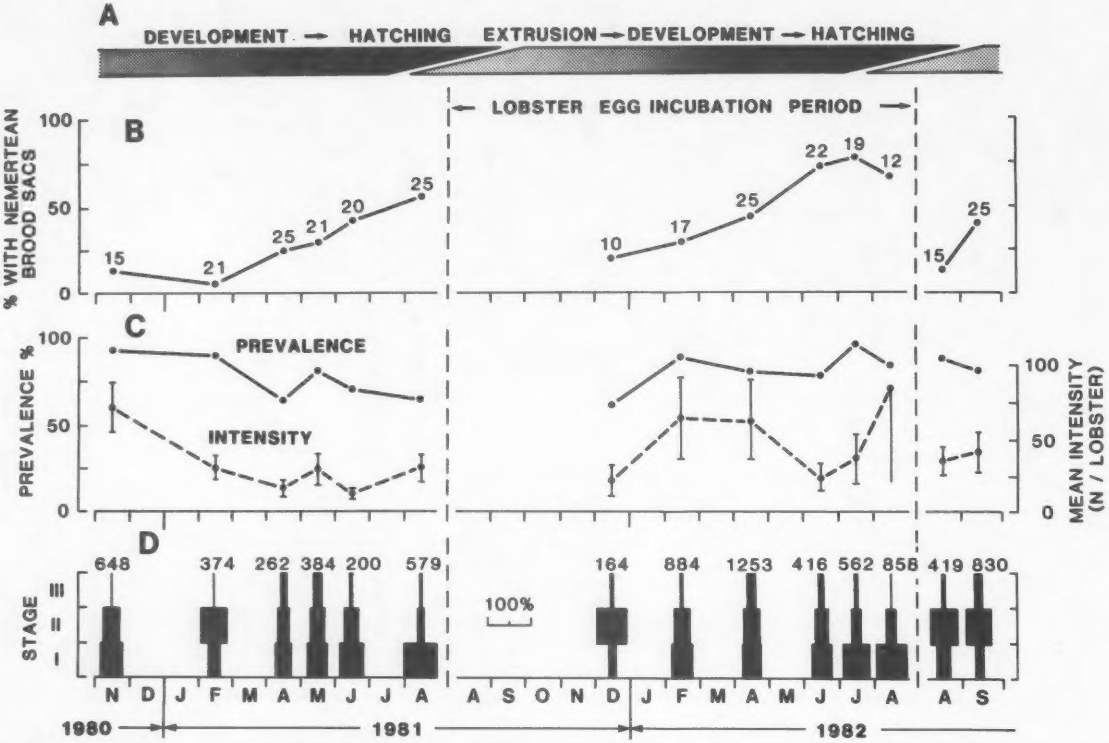

FIG. 2. Seasonal changes in the life history of *P. homari* on ovigerous lobsters collected at Grand Manan during November 1980 – September 1982. (A) Sequence and timing of events in the lobster egg incubation period; (B) prevalence of nemertean brood sacs on ovigerous lobsters; (C) prevalence and mean intensity ± SE of nemertean worms; (D) nemertean population stage structure. Numbers at each stage of maturity are expressed as a percentage of the totals for each month. Numbers indicate nemertean sample sizes. Note that the sample collected during August 1982 comprised lobsters with "old" and with "new" egg masses and data have been separated. Data on one exceptionally heavily infected lobster (14 750 nemerteans) collected in April 1981 are excluded from Fig. 2B, 2C, and 2D. Points are connected by line to indicate possible trends.

TABLE 3. Seasonal changes in the prevalence and mean intensity of *P. homari* on sexually mature nonovigerous female lobsters from Grand Manan.

Date of sample (1982)	Sample size	Prevalence	Intensity	
			Mean ± SE	Maximum
February	20	40.0	4.0±3.58	72
March	9	33.3	7.4±6.83	62
April	22	22.7	0.6±0.37	8
May	21	19.1	4.5±3.15	62
June	15	26.6	0.5±0.29	4
August	20	45.0	7.7±4.52	89

was little synchrony in the development of nemerteans belonging to the same generation.

Nonovigerous females — Data concerning seasonal changes in the occurrence of *P. homari* on mature, nonovigerous lobsters are limited to six samples collected during February–August 1982 (Table 3). Nemerteans were found on the exoskeleton and in the branchial chambers during all months, but no gravid females or nemertean brood sacs were found. Prevalence did not differ significantly between monthly samples ($p > 0.5$, df = 5), nor did mean intensity ($p > 0.5$, df = 5). Prevalence and mean intensity were, however, consistently low on nonovigerous females (19.1 to 45% and 0.5 ± 0.3 to 7.7 ± 4.5, respectively) compared with ovigerous females collected during the same period (77 to 94% and 24 ± 10 to 86 ± 63.1, respectively, Fig. 2C).

Frequency Distribution

To investigate the frequency distribution of *P. homari* among ovigerous lobsters, the mean number of nemerteans per lobster ($\bar{x}$) was related to the variance (s^2) for each sample by linear regression (Fig. 3). The relationship was adequately described by a power function of the form $s^2 = a\bar{x}^b$ or $\log s^2 = b \log \bar{x} + \log a$. The value of b represents an index of aggregation (Taylor 1961; Taylor et al. 1978). The value of b varies from zero for a regular distribution to infinity for a highly aggregated distribution. When $b = 1$, then the variance (s^2) equals the mean ($\bar{x}$), and the distribution is random. For nemertean infection on ovigerous lobsters, the slope of the regression line ($b = 2.62$) was significantly greater than unity (t-test, $p < 0.001$, df = 12). Thus, the distribution of *P. homari* among ovigerous lobsters was consistently aggregated, with a large proportion of the nemertean population on a small proportion of the ovigerous lobsters at all times of the year.

A summary of the frequency distribution of *P. homari* among all ovigerous lobsters examined ($n = 272$) is given in Fig. 4.

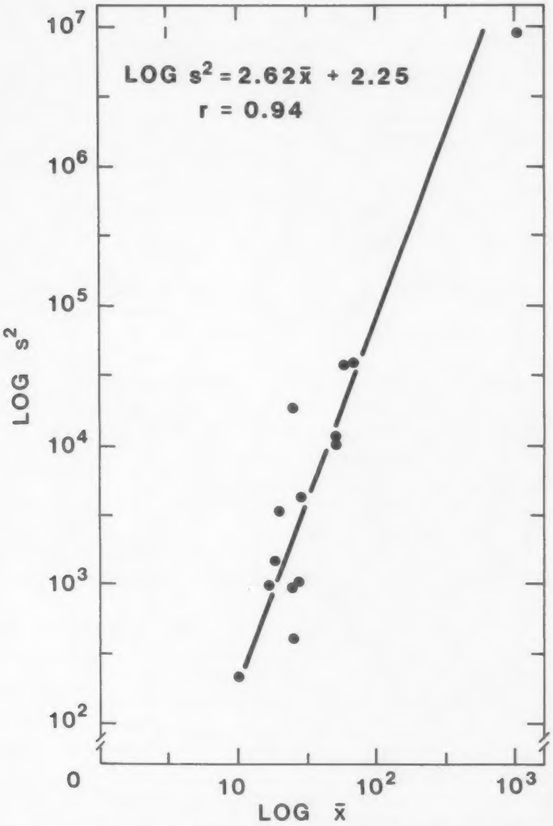

FIG. 3. Relationship between the mean ($\bar{x}$) and the variance (s^2) for counts of *P. homari* on ovigerous lobsters. The slope of the regression line ($b = 2.62$) is significantly ($p < 0.001$) greater than unity, indicating that the distribution of the nemertean on the lobster population is highly aggregated.

More than 50% of the ovigerous lobsters were infected with <10 nemerteans, whereas those with >100 were uncommon and constituted only 8% of the total number examined. Five lobsters had 266 – 14 750 nemerteans and had extensively damaged egg masses, similar to those described by Fleming and Gibson (1981) and Aiken et al. (1983); they were collected at various times of year, i.e. November 1980, April 1981, and February, July, and August 1982.

Host Size

The prevalence and mean intensity of *P. homari* on ovigerous lobsters of various sizes were determined, with size groups expressed in 10-mm CL increments (Fig. 5). In all size groups, a large proportion (68–95%) of lobsters were infected. However, prevalence and mean intensity differed significantly between size groups ($p < 0.01$, df = 6 and $p < 0.001$, df = 6, respectively) and appeared to increase with host size.

Discussion

Geographic Distribution

Our study shows that *P. homari* has a widespread geographic distribution that extends throughout Canadian Maritime waters. This nemertean has also been found on lobsters on the coast of Maine (J. S. Krouse, Maine Department of Marine Resources, West Boothbay Harbour, Maine, pers. comm.). We collected nemertean-infected lobsters at depths of 6–250 m and in areas where water temperatures can fluctuate seasonally between −1 and 20°C (Dobson and Petrie 1983). The wide depth and temperature tolerance of the nemertean suggest that its distribution may extend further, to areas not included here. Dexter (1955) did not observe nemerteans on lobsters from Connecticut during 1946.

Pseudocarcinonemertes homari infected male and female lobsters, although males were rarely infected and ovigerous females generally had more nemerteans than nonovigerous females. The greater numbers of nemerteans found on ovigerous lobsters may be attributed to *P. homari* reproducing directly on lobster egg masses (Fleming and Gibson 1981; Aiken et al. 1983, 1985) and producing several generations during a single lobster egg incubation period (this study).

There are considerable differences in the prevalence and intensity of *P. homari* on lobsters in different geographic areas. Seasonal effects could be responsible for some of the differences observed, because samples were collected from each area at slightly different times; however, *P. homari* was found on lobsters at Grand Manan throughout the year. The low prevalence at Browns and German Banks, and Northumberland Strait, contrasts with the situation at Grand Manan where 78.7% of ovigerous females were infected. The reasons for these differences are unknown. The effects of various factors such as temperature, salinity, and host density (especially ovigerous

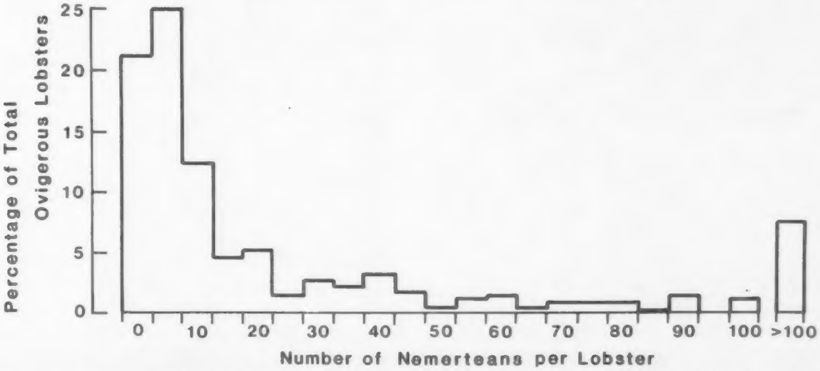

FIG. 4. Frequency distribution of *P. homari* on ovigerous lobsters collected at Grand Manan during November 1980 – September 1982 ($n = 272$).

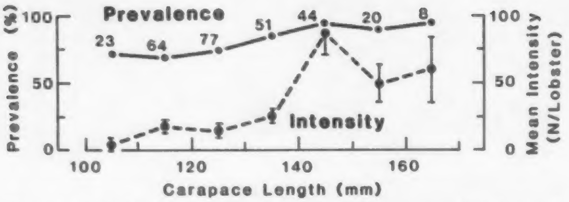

FIG. 5. Relationship between the size (CL) of ovigerous lobsters and the prevalence and mean intensity ± SE of *P. homari*. Numbers indicate sample sizes for each 10-mm CL class.

lobsters) may play an important role in the biology of *P. homari*.

Seasonal Occurrence

There was no pronounced seasonal cycle in the prevalence of *P. homari* on ovigerous female lobsters at Grand Manan. The nemertean infected a consistently large proportion (60–93%) of three consecutive populations of ovigerous lobsters (Fig. 2C). The wide differences in mean intensity between monthly samples were probably due, in part, to our small sample sizes in relation to the aggregated frequency distribution of *P. homari* (Fig. 3). Furthermore, mean intensity increased with the size of ovigerous lobsters (Fig. 5), and slight, though statistically insignificant, heterogeneity in the size composition of the lobster samples may have contributed to the apparent variability in mean intensity. Ideally, larger samples of ovigerous lobsters should have been examined, but often this presented major logistic problems and lobster fishermen were reluctant to remove larger numbers from the brood stock on their fishing grounds.

Pseudocarcinonemertes homari did not exhibit a seasonal reproductive cycle. Gravid females and brood sacs of *P. homari* were observed on ovigerous females at all times of year, suggesting that the nemertean can reproduce throughout the normal range of environmental conditions that occur in waters near Grand Manan. Fleming and Gibson (1981) reported similar findings, although they apparently examined only nine ovigerous lobsters from Grand Manan. In contrast, free-living nemerteans generally show a seasonal reproductive cycle and typically reproduce during the warmer months (Gibson 1972). Since availability of food is a major factor determining the timing of reproduction among many invertebrates, perhaps the nonseasonal reproductive cycle of *P. homari* results from the fact that lobster eggs, on which the nemertean feeds (Waddy and Aiken 1985), are available throughout the year.

The seasonal changes in nemertean life history (Fig. 2B–2D) suggest a trivoltine cycle for *P. homari* on ovigerous lobsters at Grand Manan. Our interpretation must be considered with some caution, however, because the distinction between generations is reduced by the wide variation in stage of maturity of nemerteans belonging to the same generation, and by the length of the interval between samples. Unfortunately, there are few other data on generation times of *P. homari* with which the present results can be compared. Fleming and Gibson (1981) noted that, under laboratory conditions at 4–5°C, nemertean eggs hatched in approximately 60 d, and that starved nemerteans, <2 mm in length, grew and attained full sexual maturity within 40 d. Thus, Fleming and Gibson's results give an approximate generation time of 100 d for *P. homari*, which agrees with our findings. Although a trivoltine life cycle may occur on ovigerous lobsters at Grand Manan, *P. homari* has an extensive distribution. Geographic differences in environmental factors, such as water temperature, which are known to affect the timing and duration of the lobster egg incubation period (Aiken and Waddy 1980), may also affect the life history of *P. homari*. Thus, generation times of *P. homari* on ovigerous lobsters may differ between areas.

Although a 2-yr ovarian cycle continues throughout most of the reproductive life of mature female lobsters, egg incubation usually lasts only 9–12 mo and females alternate between the ovigerous and nonovigerous condition (Aiken and Waddy 1980). Nonovigerous lobsters had a consistently lower prevalence and mean intensity of *P. homari* than ovigerous females, both at Grand Manan and in other areas, which suggests that some nemerteans either die or leave the lobster after each egg incubation cycle is completed. Female lobsters may also molt between egg incubation periods, and although the effects of molting on *P. homari* have not been explored, possibly some of the nemerteans are shed at ecdysis. Among nemerteans of the genus *Carcinonemertes* that infect crabs, there are conflicting reports about the effects of host molting. Kuris (1978) found that the crab *Hemigrapsus oregonensis* (Dana) shed most individuals of *Carcinonemertes epialti* Coe at ecdysis, whereas Wickham (1980) found that 90% of *Carcinonemertes errans* Wickham moved off the exuvium back onto the host *Cancer magister* Dana, after molting.

Maturation and reproduction of *P. homari* appeared to cease when lobster egg incubation was completed, as we did not find gravid female nemerteans or brood sacs on nonovigerous lobsters. Similarly, we found no evidence to suggest that *P. homari* reproduced on wild mature male lobsters. However, Aiken et al. (1985) found gravid female *P. homari* on a male lobster that had been isolated in a culture facility for approximately 2 yr, although this was probably an aberrant situation, created by denying the nemertean access to lobster eggs for an unusually long period.

When lobster egg incubation is completed, some individuals of *P. homari* move to the lobster branchial chambers and settle among the gill filaments (Fleming and Gibson 1981), whereas others move to protected sites on the exoskeleton where they often form "mucoid aggregations" (Aiken et al. 1985). Although mature female lobsters may remain nonovigerous for 9–12 mo (Aiken and Waddy 1980), *P. homari* can withstand prolonged periods of starvation (Fleming and Gibson 1981), and many nemerteans probably survive on nonovigerous females until new egg masses appear (assuming they are not all shed at molting). Roe et al. (1981) and Crowe et al. (1982) found that the nemertean *C. errans* on nonovigerous *C. magister* is able to absorb, directly through its body surface, primary amines that leak through noncalcified portions of the host exoskeleton. Possibly, *P. homari* acquires nutrients from nonovigerous lobsters in a similar manner.

According to Campbell and Robinson (1983), 50% of female lobsters in the Bay of Fundy attain functional maturity at a CL of 108 mm. Our results indicate that approximately 68% of ovigerous lobsters in the 100–109 mm CL group were infected with *P. homari* and that prevalence and mean intensity increased with host size (Fig. 5). Such increases can probably be attributed to several factors; larger and hence older lobsters have been exposed to potential sources of infection for longer periods than smaller ones, and the larger surface area of their exoskeletons probably increases the likelihood of infection during transmission. The fact that large lobsters molt less frequently and may undergo multiple egg extrusions without molting

(Aiken and Waddy 1980; Campbell 1983) reduces the probability of loss of nemerteans due to molting and may contribute to the higher prevalence and mean intensity among the larger lobster CL groups.

The aggregated distribution of *P. homari* among ovigerous lobster populations is similar to that known for crab-infesting nemerteans of the genus *Carcinonemertes* (Kuris 1978; Wickham 1980), and for a variety of host–parasite associations (Pennycuick 1971; Schmid and Robinson 1972; Kennedy 1968; Campbell et al. 1980). The biological mechanisms generating such distribution patterns are often complex and difficult to determine in field studies. Anderson and Gordon (1982) identified three factors that tend to create overdispersion (= aggregation), namely (1) heterogeneity in host susceptibility to infection, (2) direct reproduction within or on the host, and (3) heterogeneity in the ability of hosts to kill or remove the parasites by immunological, behavioral, or other responses.

The aggregated distribution of nemerteans may be partly due to *P. homari* reproducing directly on ovigerous lobsters (Fleming and Gibson 1981; Aiken et al. 1983; and present study) and laying several brood sacs with up to 47 eggs per brood sac on a lobster (Uhazy et al. 1985). Also, there is evidence for heterogeneity between lobsters in their ability (or willingness) to remove *P. homari* by behavioral responses that involve removal of infected eggs with chelate periopods (Aiken et al. 1985); in a culture facility, massive infestations developed only on ovigerous lobsters that did not exhibit the “cleaning” response. The aggregated distribution of *P. homari* among wild ovigerous lobsters suggests that large numbers of nemerteans, and hence extensive destruction of lobster egg masses, occur on relatively few individuals in field populations. The lobsters that we sampled were collected at various stages in the egg incubation period, and on many lobsters the nemertean infection may not have had sufficient time to develop. The apparent rarity of heavy infections in field samples may be a result of some infected lobsters removing their egg masses before such infections develop (Aiken et al. 1985). Consequently, nemertean-induced lobster egg mortality could exist in natural lobster populations and yet go largely unnoticed. However, the extent to which lobsters in the natural habitat remove their egg masses in response to *P.homari* infection is unknown. The factors that affect the differential susceptibility of wild *H. americanus* to infection and egg mortality by *P. homari* have yet to be determined.

Acknowledgments

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NOTES

Juvenile Lobster (*Homarus americanus*) Do Not Require Dietary Ascorbic Acid

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Kean, J. C., J. D. Castell, and D. J. Trider. 1985. Juvenile lobster (*Homarus americanus*) do not require dietary ascorbic acid. Can. J. Fish. Aquat. Sci. 42: 368–370.

We found no dietary ascorbic acid requirement for juvenile lobsters (*Homarus americanus*) (37–42 mg). The lobsters were fed semipurified diets containing 0, 0.6, 1.2, 2.4, or 12 g L-ascorbic acid/kg dry diet for 20 wk. At termination, the hepatopancreases were removed and assayed for ascorbic acid. There was no significant difference in growth or mortality among any of the dietary treatments. Lobsters fed the deficient diet had hepatopancreatic ascorbic acid levels that were not significantly different from animals fed the supplemented diets. Juvenile lobster, therefore, did not require dietary ascorbic acid under these experimental conditions. We suggest that juvenile lobsters do not require ascorbic acid supplementation in the diet and may be capable of de novo synthesis of this vitamin.

Nous n'avons noté aucune exigence alimentaire pour l'acide ascorbique chez des homards (*Homarus americanus*) juvéniles (37–42 mg). Les homards ont reçu pendant 20 sem une nourriture semi-purifiée contenant 0, 0,6, 1,2, 2,4 ou 12 g d'acide ascorbique/kg de nourriture (poids sec). Les hépatopancréas ont ensuite été prélevés pour dosage de l'acide ascorbique. Aucune de ces diètes n'a été source de différence significative entre les taux de croissance et de mortalité. La teneur en acide ascorbique de l'hépatopancréas des homards à diète carencée ne différait pas de façon significative de celle des homards à diète enrichie. Les homards juvéniles n'avaient donc pas besoin, dans ces conditions expérimentales, d'une nourriture contenant de l'acide ascorbique. Nous faisons l'hypothèse que les homards juvéniles ne requièrent pas de nourriture enrichie d'acide ascorbique et qu'ils peuvent synthétiser de novo cette vitamine.

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Although ascorbic acid (AsA) fulfills many metabolic requirements, its most clearly defined role is in its contribution to collagen formation. AsA is essential for the conversion of proline and lysine to hydroxyproline and hydroxylysine. The latter are required for proper collagen formation in connective tissue.

Most terrestrial vertebrates can synthesize AsA. A few species, including fruit bats (*Pteropus medius*), guinea pigs (*Cavia porcellus*), man (*Homo sapiens*), and other primates, are the exceptions. The need for dietary AsA has been established for some species of fish (Kitamura et al. 1965; Halver et al. 1969; Lovell 1973; Wilson and Poe 1973).

Chatterjee et al. (1975) suggested that most invertebrates are unable to synthesize AsA. To date, however, there are few reports to establish the AsA requirements of crustaceans. A dietary requirement for AsA has been identified for the prawn, *Penaeus japonicus* (Guary et al. 1975). A Black Death Syndrome has been attributed to AsA deficiency in the penaeid shrimp *P. californiensis* and *P. stylirostrus* (Margarelli et al. 1979; Lightner et al. 1979).

Our study was designed to investigate the AsA requirement of juvenile lobster (*Homarus americanus*).

Material and Methods

Berried female lobsters were obtained from local fishermen at Eastern Passage, Halifax, Co., N.S. Lobster larvae were hatched and reared in heated seawater (20°C) as described by Castell (1977). Seawater from Halifax Harbour ($S = 32$) was heated to 20°C and passed through a sand–gravel filter, an activated charcoal filter, a 5-μm cartridge filter (Aquapure A110), two 10-L aeration chambers, and finally a 500-L fiberglass reservoir. The flow rate of this water to each tray was about 0.5 L/m.

For each dietary treatment we used 40 juveniles. They were divided into two groups of 20 and housed in separate holding trays with individual compartments measuring 5 × 9 × 9 cm (Boghen and Castell 1979). The average initial weight of lobsters in each group was between 0.037 and 0.042 g.

The composition of the basal diet is shown in Table 1. Five

TABLE 1. Composition of the basal diet fed with or without supplemental AsA to juvenile lobsters.

Ingredient	Percentage
Vitamin-free casein	50
Gelatin	10
Corn starch	5
α-cellulose	8.8
DL-Methionine	1
Mineral mix[a]	5
Lecithin	6
Glucosamine	1
Cholesterol	1
Cod liver oil	10
Vitamin mix[b]	2
Vitamin E	0.2

[a] Bernhart–Tomarelli modified salt mix.

[b] Diluted with cellulose to provide the following (mg/kg diet): thiamine HCl, 64; riboflavin, 144; niacinamide, 512; biotin, 1.6; calcium D-pantothenate, 282; pyridoxine HCl, 48; folic acid, 19.2; menadione sodium bisulfate, 16; cobalamine (vitamin B_{12}), 43.2; L-mesoinositol, 2500; calciferol (vitamin D_2, 400 000 IU/g), 4.9; vitamin A acetate (850 000 IU/g), 100; *p*-aminobenzoic acid, 400; butylated hydroxyanisol, 150; butylated hydroxytoluene, 150. Levels of AsA were 0, 600, 1200, 2400, and 12 000 in diets 1, 2, 3, 4, and 5, respectively.

different vitamin premixes were made containing five levels of L-ascorbic acid (0, 0.6, 1.2, 2.4, and 12.0 g/kg diet). All nutrients used in the diet were obtained from ICN Nutritional Biochemicals Co., Cleveland, OH, or U.S. Biochemicals Co., Cleveland, OH. Each basal diet was thoroughly mixed with boiling water (40:60 by weight). The diets were then refrigerated until the gelatin had set. The gel that formed upon cooling was extruded with a hand press through a 2-mm die and freeze-dried for 48 h using a Virtis Freezemobile II, 10-145-V-QD and drying unit 10-MR-TR. The diets were stored frozen at −40°C in plastic bags. Sufficient amounts of each diet for 1 wk of feeding were removed and stored at −20°C until fed. All lobsters were fed ad libidum three times daily at approximately 08:00, 12:00, and 16:00 during the week and once on holidays and weekends. Uneaten food and fecal waste were removed, and molts and deaths were recorded before each feeding. At 2-wk intervals the lobsters were weighed after blotting with a paper towel to remove excess water. Lobsters were fed each of the experimental diets for 20 wk. The photoperiod was approximately 9 h light (ceiling mounted fluorescent fixtures) and 15 h dark.

At termination, the hepatopancreatic tissue was removed from each animal and assayed for AsA using the micromethod of Zannoni et al. (1974).

For comparisons among mean final wet weights, hepatosomatic indices, molt frequency, and AsA of hepatopancreases, we used the ONEWAY subprogram of the SPSS ANOVA computer program release 9.1 (Nie et al. 1975). We tested for significant differences ($\alpha = 0.05$) using the Student–Newman–Keuls procedure.

TABLE 2. Mean final weight, percent survival, hepatosomatic index (HSI), and AsA content of hepatopancreas (±SD) of juvenile lobsters fed diets containing several levels of AsA for 20 wk. There were no significant differences among dietary treatments for any of these factors ($\alpha = 0.05$).

Dietary AsA (g/kg)	Mean final weight (g)	% survival	HSI	AsA hepatopancreas (μg/g)	*n*
0.0	0.639±0.219	55.0	7.9±1.6	77.7±39.9	22
0.6	0.872±0.312	37.5	7.9±1.5	128.1±121.0	15
1.2	0.763±0.292	62.5	8.1±1.9	116.4±58.4	25
2.4	0.793±0.331	52.5	8.1±1.3	99.5±136.6	21
12.0	0.710±0.160	42.5	6.0±2.2	154.6±189.4	17

Results

There was very little difference in growth of lobsters fed different levels of AsA up to 10 wk of feeding. Although the AsA-free diet produced the lowest growth, after 20 wk of feeding this was not significantly different ($\alpha = 0.05$) from that obtained with any of the AsA-supplemented diets (Table 2).

There was no apparent relationship between the amount of dietary AsA and percent mortality (Table 2). Three of the four AsA-supplemented diets resulted in higher mortalities than the unsupplemented diet (diet 1). Again, none of the differences was significant ($\alpha = 0.05$).

There was no significant difference ($\alpha = 0.05$) in hepatosomatic indices or hepatopancreatic AsA levels among the dietary treatments (Table 2). Even after 20 wk on an AsA-free diet, lobsters had hepatopancreatic AsA levels comparable with those fed supplemented diets.

There was an average of four molts recorded for each animal throughout the course of the feeding trials. No differences in molt frequency were observed among the dietary treatments. Throughout the course of the feeding trials, the lobsters were generally healthy. No nutrition-related pathologies described for crustaceans, such as Black Death Syndrome or Molt Death Syndrome, were observed in any of the experimental animals. Gross examination of various organs at termination did not reveal any abnormality in lobsters fed different levels of AsA.

One month after termination, samples of all diets were assayed for residual AsA content. After 24 wk of storage at −40°C, greater than 50% of supplemental AsA remained. The unsupplemented diet had no detectable AsA.

Discussion

We conclude that juvenile lobsters do not require dietary AsA. Although Chatterjee et al. (1975) suggested that most invertebrates were incapable of AsA synthesis and research with other crustaceans (Guary et al. 1975; Margarelli et al. 1979; Lightner et al. 1979) demonstrated a dietary requirement for this vitamin by three penaeid species, no significant reduction in growth or survival of juvenile lobsters occurred after 20 wk of feeding with an AsA-free diet.

Many of the mortalities that occurred were likely caused by deficiencies of the dietary casein. Boghen et al. (1982) have reported that replacing casein in semipurified diets with purified crab protein (*Cancer irroratus*) resulted in significant improvement of growth and survival of juvenile lobsters. Subsequent feeding trials with AsA-free crab protein based diets resulted in improved growth and greater than 80% survival after 18 wk.

AsA found in the hepatopancreases of animals on the AsA-free diet could be derived only from a dietary source such as organisms from the seawater, or by de novo synthesis. Because the seawater was filtered through a series of three sand–gravel filters, cartridge filters, and activated charcoal before entering the experimental tanks, it is unlikely that the water provided the AsA source. Therefore we conclude that the animals are capable of de novo synthesis of AsA.

Although we found no significant effect of omitting dietary AsA on growth, survival, or hepatopancreatic AsA levels, there may be circumstances where dietary AsA would provide some benefit to lobsters. For, example in other species, dietary AsA produced a significant ameliorative effect against excessive levels of heavy metals such as copper (Fox 1975).

Our study is the first report of a nonrequirement by a crustacean for dietary AsA.

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Synthesis of Dehydroascorbic Acid by Subadult Lobsters (*Homarus americanus*)

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L. M. Desjardins, J. D. Castell, and J. C. Kean. 1985. Synthesis of dehydroascorbic acid by subadult lobsters (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 42: 370–373.

Using radiotracer studies we assessed the ability of lobsters (*Homarus americanus*) (200–300 g) to synthesize ascorbic acid from [^{14}C]glucose. No deficiency symptoms were observed in groups of 15 lobsters fed one of three semipurified diets containing 0, 1.2, and 6 g ascorbic acid/kg (diets 1, 2, and 3, respectively) for 14 wk. Six of the animals on diet 1 were studied in vivo. Five intermolt lobsters were selected from each dietary group for an in vitro study. Lobsters synthesized dehyroascorbic acid in the hepatopancreas from [^{14}C]glucose. Dietary level of ascorbic acid had no significant effect on the amount of [^{14}C]dehydroascorbic acid detected. We consider that the rate of synthesis and degradation may be affected by the molt cycle.

Nous avons évalué par la technique des radiotraceurs la capacité de homards (*Homarus americanus*) (200–300 g) à synthétiser l'acide ascorbique à partir de [^{14}C]glucose. Aucun symptôme de carence n'a été noté chez des groupes de 15 homards recevant pendant 14 sem une nourriture semi-purifiée contenant 0, 1,2 ou 6 g d'acide ascorbique/kg (diètes 1, 2 ou 3). Six des homards recevant la diète 1 ont fait l'objet d'une étude in vivo. Cinq homards en période d'intermue de chaque groupe ont été choisis pour une étude in

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vitro. Les homards synthétisaient l'acide déhydroascorbique dans l'hépatopancréas à partir du [^{14}C]glucose. La teneur alimentaire en acide ascorbique n'a pas eu d'effet significatif sur la quantité d'acide [^{14}C]déhydroascorbique décelée. Nous pensons que le cycle de mue peut avoir un effet sur les taux de synthèse et de dégradation.

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Many species of fish require a dietary source of ascorbic acid (AsA). Channel catfish, *Ictalurus punctatus* (Lovell 1973; Wilson and Poe 1973; Andrews and Murai 1975), rainbow trout, *Salmo gairdneri* (Hilton et al. 1977; Kitamura et al. 1965), and coho salmon, *Oncorhynchus kisutch* (Halver et al. 1969) fed diets free of AsA supplementation had poor growth and high mortalities. Deficiency symptoms such as lordosis, scoliosis, and impaired wound healing due to decreased collagen formation were noted. In contrast, carp, *Cyprinus carpio*, had normal growth and survival, and no deficiency symptoms were observed (Sato et al. 1978).

Yamamoto et al. (1978) investigated the activity of gulonolactone oxidase, the terminal enzyme of the AsA biosynethetic pathway, in different fish species. Catfish, *Parasilurus asotus*, had low enzyme activity in the liver and kidney. Other species, including rainbow trout, showed little or no activity. Carp, however, had very high activity in the hepatopancreas. Ikeda and Sato (1964) earlier demonstrated [^{14}C]AsA synthesis from precursors such as ^{14}C-D-glucuronolactone and ^{14}C-D-glucose in carp. Similar radiotracer studies on rainbow trout were inconclusive (Hilton et al. 1978). The need for exogenous AsA appears to be dependent on the ability to synthesize AsA.

Little is known about AsA requirement and synthesis in crustaceans. Prawns, *Penaeus japonicus*, showed better growth when fed diets not supplemented with AsA but mortalities were high (Deshimaru and Kuroki 1976). Decoloration of the carapace, abdomen, and the tips of the walking legs were some of the deficiency symptoms observed.

Margarelli et al. (1979) reported that juvenile penaeid shrimp, *P. californiensis* and *P. stylirostris*, fed diets without an AsA supplement had reduced growth and high mortalities accompanied by a Black Death Syndrome. This disease is characterized by melanized lesions in connective tissues. These penaeid shrimps were also incapable of wound repair under similar experimental conditions (Lightner et al. 1979).

Juvenile lobsters fed an AsA-free semipurified diet had normal growth and survival, and deficiency symptoms such as Black Death were not observed (Kean et al. 1985). The levels of AsA in the hepatopancreas were not significantly different from the controls.

The purpose of this study was to investigate de novo synthesis of AsA in lobsters from [^{14}C]glucose.

Materials and Methods

Forty-five lobsters weighing between 200 and 300 g were taken from the Prince Edward Island coast. They were placed in flushing-trays (approximately 2.4 × 0.3 × 0.2 m) supplied by Marine Lobster Farms Inc., Victoria, P.E.I. These fiberglass trays contained nine dividers to separate the lobsters and prevent cannibalism. Filtered seawater was maintained at 15°C and flowed at a constant rate of $2\ \mathrm{L \cdot min^{-1} \cdot tray^{-1}}$. The photoperiod followed the natural light cycle (May–August).

The lobsters were fed semipurified diets containing AsA at the level of 0, 1.2, and 6 g/kg (diets 1, 2, and 3, respectively). The source of ingredients and composition of the diets were the same as in Kean et al. (1985) with a few alterations (Table 1). These were prepared fresh monthly and stored at −40°C. The lobsters were fed twice daily over a period of 14 wk at the rate of 2% body weight per day.

For the in vivo experiments, six lobsters at different stages of the molt cycle were taken from the group that was fed diet 1. They were force fed 1.1×10^5 Bq of uniformly labelled [^{14}C]glucose (New England Nuclear, Boston, MA). The labelled glucose was dissolved in 1 mL of a hot 15% gelatin solution. This mixture, after gelling in a disposable 1-mL syringe, was injected into the oral cavity of the lobster and none was regurgitated.

The lobsters were incubated at 20°C for 48 h in a 20-L glass aquarium with a removable Plexiglas lid. Oxygen was supplied with an airstone and the expelled air was bubbled through three 2 mol NaOH/L traps in order to collect $^{14}CO_2$. At the end of the incubation period, 1-g tissue samples were taken at six different locations of the hepatopancreas: right and left anterior, central, and posterior lobes. The tissues were quickly homogenized in 4 mL of 5% trichloroacetic acid using a Potter–Elvehjem homogenizer. The supernatant was filtered through a Pasteur pipette with a glasswool plug; 150 μL of this filtrate was streaked onto a silica gel G thin layer chromatography (TLC) plate that had previously been sprayed with 3% metaphosphoric

TABLE 1. Composition of the experimental diet.

Ingredient	Percentage
Vitamin-free casein	50
Gelatin	10
Corn starch	5
Bernhart–Tomarelli salt mix	5
α-Cellulose	8.8
Cholesterol	1
Glucosamine	1
DL-Methionine	1
Lecithin	6
Cod liver oil	10
Vitamin mix[a]	2
Vitamin E	0.2

[a] Diluted with celite to provide the following (mg/kg diet): thiamine HCl 64; riboflavin, 144; niacinamide, 512; biotin, 1.6; calcium D-pantothenate, 282; pyridoxine HCl, 48; folic acid, 19.2; menadione sodium bisulfate, 16; cobalamine (vitamin B_{12}), 43.2; L-mesoinositol, 2500; calciferol (vitamin D_2, 400 000 IU/g), 4.9; vitamin A acetate (850 000 IU/g), 100; *p*-aminobenzoic acid, 400; butylated hydroxyanisol, 150; butylated hydroxytoluene, 150. Levels of AsA were 0, 1200, and 6000 in diets 1, 2, and 3, respectively.

TABLE 2. ^{14}C radioactivity of DAsA extracted from the hepatopancreas after 12 h of incubation with [^{14}C]glucose in vitro (means ± SD of 15 hepatopancreatic lobes taken from five lobsters in dpm/g × 10^3). Differences not significant ($p > 0.05$).

	Diet 1 (0 g/kg)	Diet 2 (1.2 g/kg)	Diet 3 (6 g/kg)
^{14}C radioactivity	2.44±0.52	4.11±1.81	4.37±1.65

acid and activated at 100°C for 30 min. The streaks were dried under a stream of nitrogen. The TLC plates were developed in acetonitrile–butyronitrile–water (66:33:2, v/v) as described by Saari et al. (1967).

Standard dehydroascorbic acid (DAsA) and AsA were co-chromatographed for every TLC plate. The DAsA band was moistened with 1 mL of water, and then scraped into a scintillation vial containing 15 mL of scintillation cocktail (Aquasol 2, New England Nuclear, Boston, MA). The samples were counted on a Packard Tri-carb liquid scintillation spectrometer 3255 equipped with an automatic external standard.

For the in vitro experiment, five intermolt lobsters were selected from each dietary treatment; 1-g samples were taken from the right anterior, central, and posterior lobes of the hepatopancreas. Each sample was placed into a Gilson respirometer flask containing lobster hemolymph medium (Paterson and Stewart 1974) and 3.7 × 10^3 Bq of [^{14}C]glucose. The center well of each flask had filter paper soaked with 2 mol NaOH/L. The DAsA was extracted by the same described procedures after a 12-h incubation at 15°C in a Gilson respirometer (model No. GR 20 AG11). The data were statistically analyzed by Tukey's procedure (Snedecor and Cochran 1980).

Results

There were no deficiency symptoms after 14 wk in the lobsters fed the AsA-free diet. Incubation of the hepatopancreatic tissues with [^{14}C]glucose resulted in the synthesis of significant amounts of [^{14}C]DAsA in all dietary treatments (Table 2). [^{14}C]AsA was not detected in significant levels in any treatment. There was no significant effect of the dietary AsA levels on the rate of [^{14}C]DAsA synthesis ($p > 0.05$).

The in vivo study showed that the ^{14}C radioactivity in the hepatopancreas associated with AsA was not present at a detectable level; however, the [^{14}C]DAsA counts were significant (Table 3). These results agree with those found in the in vitro study, i.e. lobsters are capable of synthesizing the oxidized form of AsA from glucose.

In the in vitro study there was high variability among lobsters in the level of [^{14}C]DAsA detected. This appeared to be related to the molt cycle. The highest values occurred in the late intermolt and premolt stages, and the lowest was in late postmolt. The late intermolt lobster had a very high standard deviation which was due to a higher concentration of [^{14}C]DAsA in the posterior and central lobes compared with the frontal lobes. We do not know if this was just an isolated case or whether the distribution of the vitamin changes under certain physiological circumstances. The other animals had an even distribution of the labelled DAsA in their hepatopancreases.

The in vitro data were analyzed to see if there was a difference between the lobes in their content of [^{14}C]DAsA (Table 4). In these intermolt lobsters the anterior and central portions of the hepatopancreas had higher levels of [^{14}C]DAsA than the posterior lobes. This difference, however, was not statistically significant ($p > 0.05$).

Discussion

Juvenile lobsters have not demonstrated dietary requirement for AsA (Kean et al. 1985). In our study, the lobsters synthesized significant amounts of [^{14}C] DAsA from [^{14}C]glucose, but labelled AsA was not detected either in vivo or in vitro. Halver et al. (1975) suggested that ascorbate-2-sulphate is a storage form in fish. Possibly, DAsA is the storage form in lobsters. A dehydroreductase has been isolated in carp hepatopancreas (Yamamoto et al. 1977). This enzyme catalyzes the transfer of hydrogen from reduced glutathione to DAsA. A similar enzyme may exist in lobster hepatopancreas providing the reduced AsA necessary to meet the animal's metabolic needs. If this dehydroreductase were present in lobsters, it is possible that dietary AsA supplements would result in feedback inhibition. This might explain the higher (though not statistically significant) levels of [^{14}C]DAsA in the hepatopancreas of lobsters fed AsA supplements.

Juvenile penaeid shrimps fed AsA-deficient diets developed deficiency symptoms such as Black Death (Margarelli et al. 1979). Older shrimps of this species as well as juvenile lobsters did not have deficiency symptoms under similar experimental conditions (Margarelli et al. 1979; Kean et al. 1985). As a result, it is thought that the appearance of deficiency symptoms is influenced by species differences as well as the effect of age or size on the ability to synthesize AsA in vivo.

The present study shows that the lobster hepatopancreas is a site of DAsA synthesis and storage. The different lobes of the hepatopancreas are capable of making the oxidized form of this vitamin to the same extent; thus, the hepatopancreas apparently does not have a specific area for the synthesis of DAsA.

Only one animal was used at each molt stage for the in vivo study. The rate of [^{14}C]DAsA synthesis increased over the molt cycle, from the low at 2 wk postmolt to peak levels just prior to molting. Clearly, these results must be repeated with greater numbers of lobsters at each molt stage. Based on our limited results, however, we suggest that the rate of synthesis and degradation of this vitamin is related to molting. Guary et al. (1975) studied the relationship between whole body AsA concentration and the molt cycle of *Palaemon serratus*. The animals

TABLE 3. ^{14}C radioactivity of DAsA extracted from the hepatopancreas 48 h after force feeding [^{14}C]glucose in vivo (means ± SD of six hepatopancreatic lobes taken from one lobster in each molt stage in dpm/g × 10^3; overall mean of six lobsters 2.84 ± 1.68).

	Intermolt			Postmolt		
	Mid	Late	Premolt	2 h	12 h	2 wk
^{14}C radioactivity	2.86±0.74	3.90±2.15	4.93±0.97	2.95±0.35	1.47±0.19	0.92±0.27

TABLE 4. ^{14}C radioactivity of DAsA extracted from different lobes of the hepatopancreas after 12 h of incubation with $[^{14}C]$glucose in vitro (means ± SD taken from five lobsters in dpm/g × 10^3). Differences not significant ($p > 0.05$).

	Anterior lobe	Central lobe	Posterior lobe
^{14}C radioactivity	4.33±1.96	4.16±1.75	2.51±1.43

had the highest concentration just before premolt, and the lowest was in the later part of the postmolt stage. Their results correspond with our findings where the highest amount of $[^{14}C]$DAsA was isolated during late intermolt and premolt, and the lowest was in last postmolt.

The levels of $[^{14}C]$DAsA detected in the hepatopancreas were not significantly reduced by dietary AsA even when this vitamin was fed at five times the level normally supplemented to lobster diets.

We conclude that lobsters do not develop AsA deficiency symptoms because they are capable of synthesizing sufficient amounts of DAsA in the hepatopancreas.

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Radiotracer Estimation of Microbial Biomass in Lake Sediment

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The biomass of sediment organisms can be measured by allowing carbon tracer to distribute itself through sediment cores. Application of this method to sediment from Marion Lake, British Columbia, indicated that most of the sediment microorganisms were concentrated in the top 2 cm of sediment, where the total biomass of microorganisms was estimated to be 183 μg C/cm^2. The radiotracer estimate compared favorably with independent measurements based on ATP and direct microscopic counts of sediment microorganisms.

On peut quantifier la biomasse des organismes sabulicoles en permettant la distribution d'un traceur au carbone dans des carottes sédimentaires. L'application de cette méthode à des sédiments recueillis dans le lac Marion (C.-B.) a révélé que la plupart des microorganismes étaient concentrés ans les premiers 2 cm où la biomasse total s'élevait à 183 μg C/cm^2. Cette valeur se rapproche de quantifications indépendantes basées sur la détermination du volume d'ATP et le dénombrement des microorganismes à l'aide d'un microscope.

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Estimating the biomass of sediment microorganisms is basic to studying their ecology, but it is not a simple matter. The most straightforward approach would be to separate microorganisms from the sediment and weigh them or measure their carbon content. Although there are possibilities for separation using sonification (Puleo et al. 1967), complete separation has not yet proven feasible, particularly when the microorganisms are thoroughly enmeshed with detritus. Rodina (1972), Sorokin and Kadota (1972), Collins (1977), and Jones (1977) have reviewed current methodologies for measuring microbial biomass, and two methods appear to provide the best estimates: (1) direct counts by fluorescent microscopy; (2) ATP assay.

Unfortunately, even these two methods have some serious limitations. Direct counts may fail to distinguish active microorganisms from spores; and minor alterations in fluorescent staining technique can sometimes lead to significant changes in the count (Jones 1974). Furthermore, translating counts to biomass requires an estimation of the size distribution of the microbial population and conversion factors from cell volume to biomass, which may not be known precisely for the samples in hand. ATP assay has been used to estimate the total living biomass in a sample, based on the apparent similarity of the carbon/ATP ratio for a wide variety of organisms (Holm-Hansen and Booth 1966). However, the precision of this method is still uncertain because the carbon/ATP ratio has in fact been observed to vary from 25 to 2000, depending upon the organism and environmental conditions, though the carbon/ATP ratio appears to be 200–300 for many bacteria (Karl 1980).

This report describes a radiotracer approach to measuring the biomass of sediment microorganisms which may overcome some of the limitations of existing methods.

Methods

The measurement of biomass with radiotracers is based upon the principle that, given sufficient time, a radiotracer will distribute itself throughout an ecosystem in proportion to the element it is tracing. If a carbon tracer is introduced to a sediment core sample, the tracer should eventually distribute itself in proportion to the actively circulating carbon in the core. The vertical distribution of the tracer should reflect the vertical distribution of actively circulating carbon in the sediment core, and the distribution of tracer between particulate and dissolved fractions should reflect the amount of carbon in living biomass compared with other forms of actively circulating carbon such as CO_2. If the quantity of dissolved inorganic carbon (DIC) can be measured directly, then it should be possible to infer the absolute amount of carbon in the living biomass by using the following simple proportion:

$$\frac{\text{Total living particulate carbon}}{\text{Total DIC}} = \frac{\text{Tracer in particles}}{\text{Tracer in DIC}}.$$

Description of the sediment — The sediment in this study was collected at a water depth of 1 m in Marion Lake, a small, shallow, oligotrophic lake in British Columbia (Efford 1972; Hall and Hyatt 1974). The sediment was 40% organic matter by dry weight and originated as mineral particles, aquatic macrophytes, epibenthic algae, leaves, and other forms of detritus that washed into the lake and were consumed and reconsumed by detritivores such as the amphipod *Hyalella azteca*. The top of the sediment was bare except for occasional strands of filamentous green algae (Gruendling 1971). Although fungi were numerous among newly decomposing leaves at the lake shore, they were not a significant part of the microflora in the more thoroughly processed detritus which occurred at a depth of 1 m (Dick 1971).

The sediment consisted largely of detritivore feces, small porous particles averaging 50–200 μm in diameter and containing macrophyte and diatom fragments held together by amorphous brown organic matter. Fluorescent microscopy of sectioned sediment revealed an abundance of bacteria (typically 1 μm in diameter) and microscopic blue-green algae (typically 2–5 μm in diameter) adhering to the outer and inner surfaces of the sponge-like sediment particles. The bacteria were much more numerous than the blue-green algae and tended to occur in clusters of about 100 individuals. The surface covered by bacteria appeared to be only a fraction of the total surface area inside and outside the particles. In addition to algae and bacteria, the living biomass in the sediment included protozoa and tiny animals such as rotifers, nematodes, and copepods, restricted for the most part to the aerobic zone in the top 2 cm of sediment.

Experimental procedure — A series of sediment core samples was taken with as little disturbance as possible in clear plastic cylinders 1.8 cm in diameter and 6 cm long with 1 cm of air and 1 cm of water above the sediment. The water above the surface of the sediment in two of the cylinders was sampled for dissolved oxygen. The sediment interstitial water was extracted by suction filtration, and along with surface water, was sampled to measure DIC and dissolved organic carbon (DOC) with an infrared gas analyzer. The same measurements were made on additional cores after they were stoppered at the top and bottom for 2 or 3 wk as described below.

Sediment samples were taken from two of the cores at 1-cm intervals to a depth of 5 cm below the mud–water interface. The samples were placed in flasks containing [^{14}C]glucose to measure microbial activity, $K_{\max}$ of Michaelis–Menton kinetics, following the procedure described by Hall et al. (1972) for measuring heterotrophic uptake of organic solutes by mixed sediment. Samples from two additional cores were placed in flasks containing $^{14}CO_2$ to measure microbial activity based on CO_2 uptake.

The rest of the cores were used to estimate biomass by

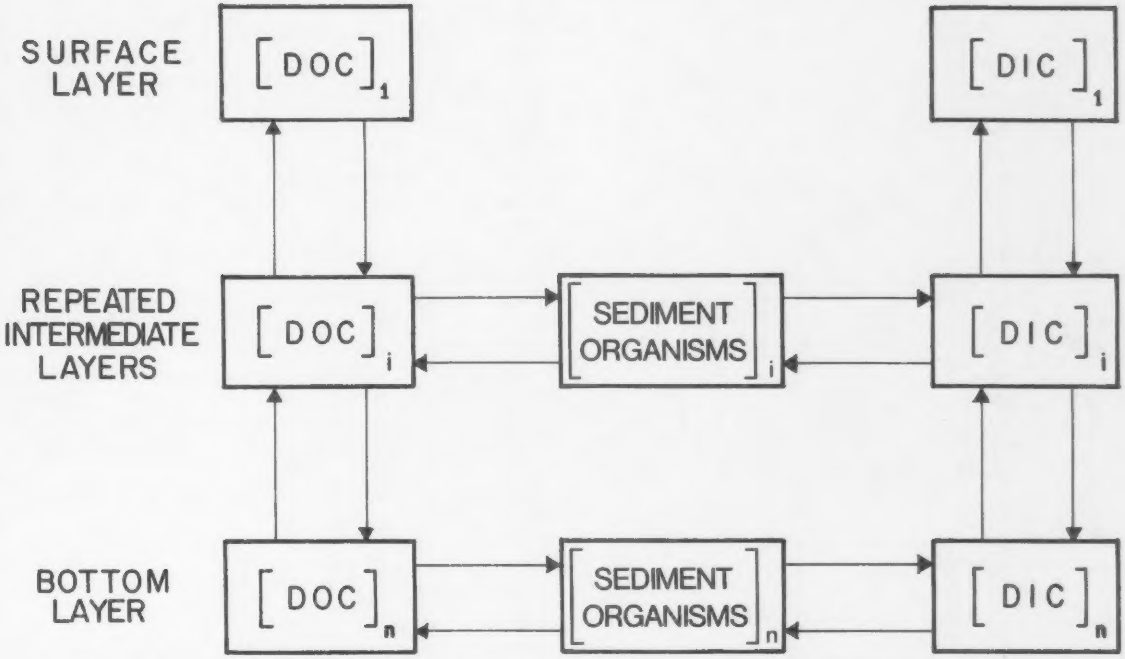

Fig. 1. Conceptual model for the vertical movement of carbon tracer through the sediment and between dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and particulate (i.e. living organism) fractions at any one depth.

allowing a carbon tracer to distribute itself through the core. [^{14}C]Glucose and $^{14}CO_2$ were considered particularly appropriate substrates for introducing carbon tracer to the cores because they are utilized by a great variety of microorganisms (Strzelczyk et al. 1974; Atlas and Bartha 1981). Carbon tracer was also introduced as [^{14}C]acetate.

[^{14}C]Glucose (37 kBq) was placed in the surface water of three of the cores, and 37 kBq of [^{14}C]glucose was injected at the same time into the bottom (i.e. 4 cm below the sediment surface) of three additional cores. One of the three cores of each treatment was injected throughout with formalin and served as a killed blank. The cores were held for 3 wk at 15°C under a 12 h light : 12 h dark cycle at 15°C. The cylinders were stoppered at both ends, but the top stopper was removed for a few seconds each day to renew the air bubble above the water and maintain aerobic conditions at the sediment surface. $^{14}CO_2$ (148 kBq in the form of [^{14}C]bicarbonate) was placed in the surface water of three additional cores, and 37 kBq of [^{14}C]acetate was placed in the surface water of another three cores. The cores receiving $^{14}CO_2$ and [^{14}C]acetate were treated the same as those receiving glucose except they were terminated after 2 wk instead of 3 wk.

The experiment was terminated by freezing the cores in liquid nitrogen and slicing into 0.5-cm segments. Each segment was separated into particulate, DOC, and DIC fractions by the following procedure. First, a segment was placed in 10 mL of distilled water and acidified to drive off CO_2, and the CO_2 was collected in glass fiber filters saturated with hyamine hydroxide. The remaining solution was filtered through a 0.22-μm Millipore filter. The glass fiber filters (containing DIC) and a subsample of the filtrate (containing DOC) were each placed in vials of Bray's solution for scintillation counting. The Millipore filter (which contained the particulate fraction) was combusted to CO_2 and prepared for scintillation counting by the method of Burnison and Perez (1974).

Carbon tracer in the sediment fraction was assumed to represent the amount of tracer in sediment organisms. This assumption requires that significant quantities of tracer did not leak from the particulate to DOC fraction due to cell lysis during the freezing and thawing process. It also assumes that significant quantities of tracer were not present in particulate materials other than living organisms (e.g. detritus particles). Tracer activity in the sediment fraction of the formalin blanks was negligible, indicating that tracer activity in the sediment fraction was due almost entirely to uptake by living organisms rather than physical processes such as adsorption of tracer on sediment particles. It was also verified by autoradiography that carbon tracer was instantly taken up by sediment microorganisms. Carbon tracer in the particulate fraction could be in the microorganisms themselves or in extracellular organic matter such as mucopolysaccharides, whose deposition on sediment particles is mediated by microorganisms (Hobbie and Lee 1980).

Tracer diffusion equation — It is easy to determine whether tracer equilibrium has been reached; if it has, the vertical distribution of tracer in the cores is the same regardless of whether it was introduced at the top or bottom of the cores. If equilibrium has not occurred, then two distinct processes must be taken into account to interpret the results (Fig. 1). First, tracer in solution (i.e. DIC and DOC) diffuses vertically through a sediment core. Second, at each depth there is an exchange of tracer between living organisms in the sediment and tracer in solution.

Although the vertical diffusion process is spatially contin-

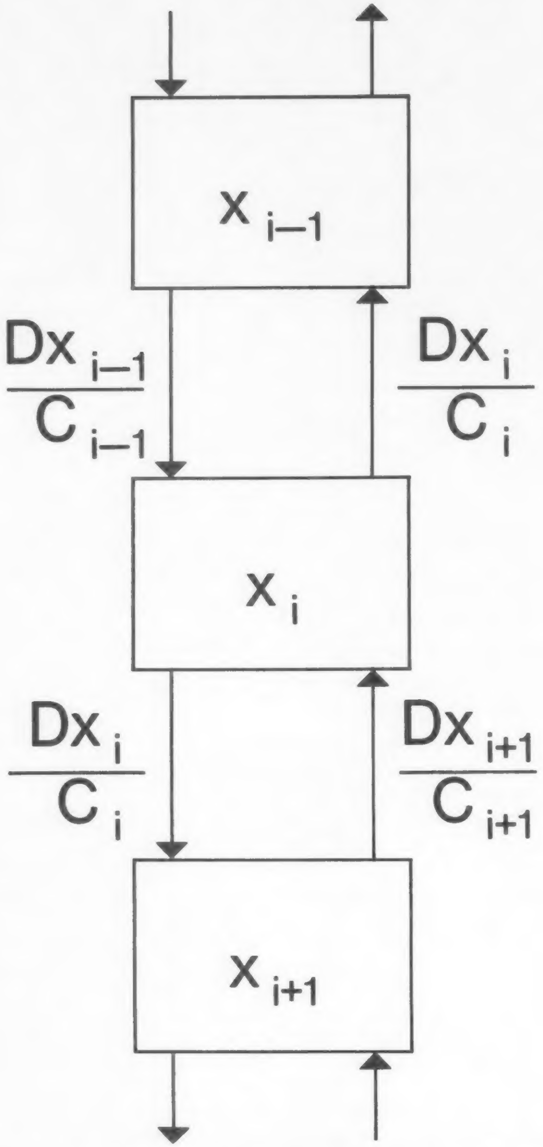

FIG. 2. Model of the vertical movement of carbon tracer with DIC, DOC, and particulate carbon pooled into a single category (C_i) (x_i is the amount of carbon tracer and D is a diffusion coefficient).

uous, it is convenient as an approximation to divide the process into vertical segments which correspond to the slices used to sample a core at the end of the experiment. The process can then be described in terms of the movement of tracer between each segment and its neighbor segments (Fig. 1). At this point it is useful to make a simplification, which assumes that equilibration between microorganisms and dissolved carbon at any one depth in the core is fast enough to allow separate consideration of (a) the relatively rapid exchange between living organisms and dissolved carbon (horizontal arrows in Fig. 1) and (b) the relatively slow vertical diffusion process. This important assumption — a rapid equilibrium between microorganisms and dissolved carbon at each depth in the sediment — was verified by injecting broadly labelled DOC into a series of cores and sampling the interstitial water at hourly intervals. Most of the labelled DOC disappeared within an hour, and the tracer approached equilibrium well within a few hours. When $^{14}CO_2$ was injected into cores or placed into the water above the sediment, the $^{14}CO_2$ approached equilibrium within 24 h.

The assumption of horizontal equilibrium allows us to suppose that at the end of a 2- or 3-wk experiment the distribution of carbon between microflora, DOC, and DIC within a vertical layer is simply in proportion to the distribution of carbon tracer in that sediment, even if the tracer has not yet reached vertical equilibrium. We are then free to concentrate on the vertical diffusion process, which may not reach equilibrium so quickly. Each box in Fig. 2 combines microorganisms, DOC, and DIC into a single category: the total mass of actively circulating carbon (C_i) in the ith vertical sediment. C_i does not include carbon in nonliving detritus and humic compounds, which are not actively circulating.

The vertical diffusion process may then be described by the following "diffusion equation":

$$\frac{dx_i}{dt} = D\left[\frac{x_{i+1}}{C_{i+1}} + \frac{x_{i-1}}{C_{i-1}} - \frac{2x_i}{C_i}\right]$$

where x_i = the total amount of carbon tracer in the ith vertical layer and D = a diffusion coefficient which results from both physical and biological processes (including the stirring effect of small animal activity).

The first two terms of the equation represent the diffusion of tracer into the ith layer from the two adjacent layers (Fig. 2), and the last term represents a corresponding diffusion of tracer out of the ith layer. The diffusion equation describes the vertical movement of tracer through a sediment core, a key feature of the process being that the movement of tracer through the core is retarded when the tracer is taken up by microorganisms that must again release it into solution before it can diffuse to an adjacent vertical segment.

We want to ask, "What values of D and C_i generate a solution whose x_i are closest to the observed vertical distribution of carbon tracer?" The mathematical problem is to fit the system of differential equations to the experimental data, in our case the vertical distribution of tracer 2 or 3 wk after introducing the tracer into the top and bottom of different sediment cores. The diffusion equation was fitted by means of a computer program for tracer kinetics described by Marten et al. (1975).

Once calculated, the C_i provide relative estimates of the total actively circulating carbon (DOC + DIC + living organisms) in each vertical layer. Assuming horizontal equilibrium within each layer, the carbon in each layer can be assigned in direct proportion to the amount of tracer in the DOC, DIC, and particulate fractions. Absolute values can be assigned on the basis of direct measurements of DIC.

Results

The oxygen concentration of the water above the sediment remained near saturation during the cores' 2- or 3-wk incubation periods. The average DOC content of the top 5 cm of sediment interstitial water was 14 μg C/mL immediately after removal from the lake bottom and 15 μg C/mL after 3 wk. Average DIC remained at 7 μg C/mL.

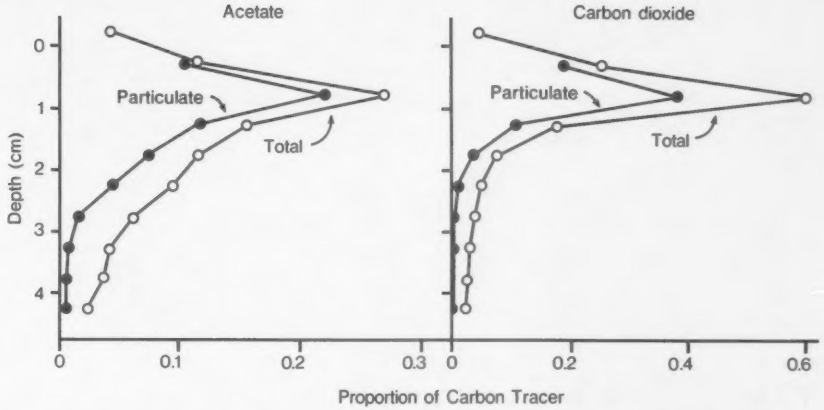

FIG. 3 Vertical distribution of carbon tracer (x_i) 2 wk after introduction as [^{14}C]acetate or $^{14}CO_2$ to the water above the sediment. "Particulate" reflects the amount of tracer in sediment organisms. "Total" includes DIC and DOC fractions as well. The top point corresponds to water immediately above the sediment.

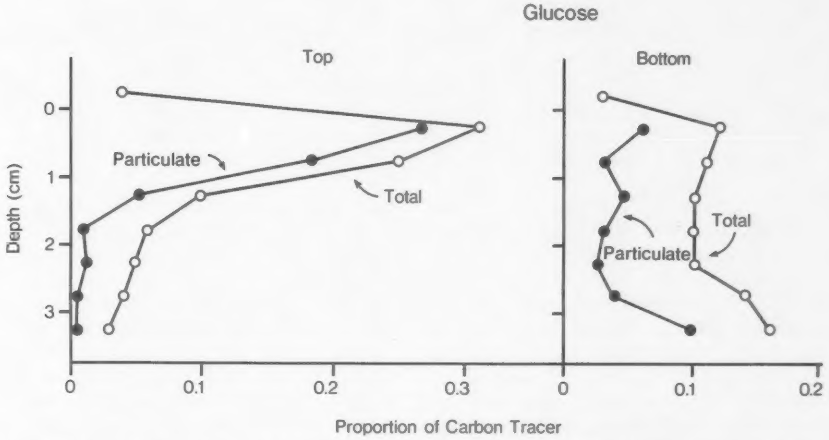

FIG. 4. Vertical distribution of carbon tracer (x_i) 3 wk after introduction as [^{14}C]glucose to the water above the sediment (top) or injection at the bottom of a sediment core (4-cm depth). Other conventions as in Fig. 3.

Vertical distribution of the living biomass — The vertical distribution of tracer 2 or 3 wk after being introduced into the top of the cores was the same whether the initial substrate was acetate, CO_2, or glucose (Fig. 3, 4), but the vertical distribution of tracer introduced at the top was radically different from tracer introduced at the bottom (Fig. 4). This meant that vertical equilibrium could not be assumed, so the diffusion equation was used to interpret the results in Fig. 4. The differences between the vertical distribution of tracer introduced at the top and bottom of cores appears to be in part a consequence of a very slow rate of vertical tracer diffusion in solution, since the tracer in formalin blanks did not distribute evenly through the cores in a 3-wk period. However, if only slow diffusion were responsible for the difference, the vertical distribution of tracer introduced from the bottom would be the mirror image of tracer introduced from the top. This was not so (Fig. 4), apparently because the carbon tracer was also intercepted by the sediment's living biomass.

Figure 5 shows the fit of the diffusion equation to the data in Fig. 4. The fit was made simultaneously to the vertical distribution of total carbon tracer (particulate plus DIC and DOC) in cores to which [^{14}C]glucose was introduced at the top and cores to which [^{14}C]glucose was introduced at the bottom. The fit is so close that the estimated values for relative C_i, shown as total carbon in Fig. 5, generated expected values of vertical tracer distribution (x_i) that could not be plotted separately from the observed values of x_i in Fig. 4. The close fit suggests that even though tracer movement is a consequence of complex and spatially heterogeneous processes, the diffusion equation can provide a satisfactory empirical description of tracer movement through a sediment core, thereby providing a basis for measuring the vertical distribution of total actively circulating carbon in the core.

Once the total actively circulating carbon (i.e. living organisms, DIC, and DOC) at each depth in the sediment had been estimated, it was then necessary to estimate the amount of that

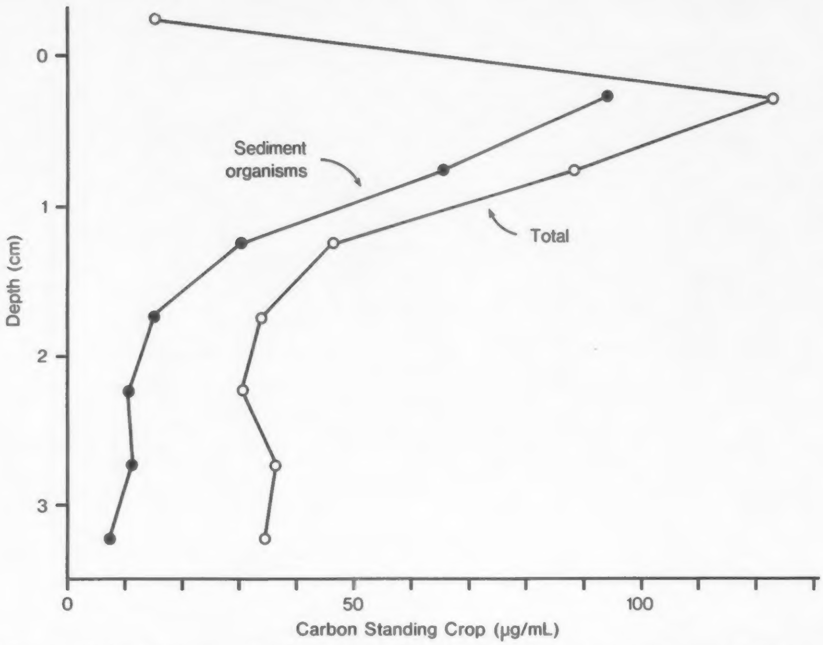

FIG. 5. Estimated biomass of sediment organisms. Also shown is C_i, the estimated vertical distribution of total actively circulating carbon (i.e. sediment organisms plus DIC and DOC). The top point corresponds to water immediately above the sediment.

carbon which could be attributed to living organisms. Drawing on the assumption of tracer equilibrium between particulate and solution fractions at any particular depth within the sediment, the total carbon at each depth was assigned to living biomass in simple proportion to the average percentage of tracer observed in the particulate fraction at that depth in the core. Figure 5 shows that most of the living biomass was concentrated in the top 2 cm of sediment, though smaller quantities persisted to greater depths. The biomass in the water above the sediment was considerably less than in the sediment below. Like the living biomass, actively circulating DOC was concentrated near the sediment surface, but DIC was more uniformly distributed throughout the sediment with a slight peak near the surface. There was less carbon tracer in DOC than in DIC, particularly at greater depths. However, infrared carbon analysis measured overall DOC concentrations to be greater than DIC, suggesting that some of the DOC, particularly at greater depths, was not circulating and therefore not labelled with tracer.

The absolute values in Fig. 5 were assigned so the estimated overall amount of DIC was the same as the overall amount measured directly by carbon analysis of interstitial water from the cores (i.e. 7 µg C/mL). The biomass in the top 5 cm of sediment was estimated to be 250 µg C/cm^2, nearly all of it (200 µg C/cm^2) in the top 2 cm. Subtracting 17 µg C/cm^2 for meiofauna (based on direct counts by Hoebel 1978), the estimated biomass of microorganisms in the top 2 cm is 183 µg C/cm^2. Virtually all the microorganism biomass should be bacteria and algae, since the estimated protozoan biomass (based on direct counts by Kool 1975) was only 0.1 µg C/cm^2.

Discussion

The radiotracer estimates of living biomass in Fig. 5 can be compared with estimates obtained by other methods on sediment samples from the same location. The vertical distribution of biomass in Fig. 5 is similar to that of microbial activity in Fig. 6, and it is also similar to the vertical pattern of bacterial counts reported by Hall and Hyatt (1974). The biomass estimate of 183 µg C/cm^2 for microorganisms in the top 2 cm of sediment is close to an estimate of 150 µg C/cm^2 based on ATP (Perry 1974). It is somewhat higher than an estimate of 119 µg C/cm^2 based on direct count estimates of 79 µg C/cm^2 for bacteria (Perry 1974) and 40 µg C/cm^2 for algae (Greundling 1971).

Although the general agreement among these methods is reassuring, it does not prove that any one of them is measuring the biomass of sediment microorganisms with a high degree of precision. The radiotracer method will require considerably more validation, and possibly substantial modification, before it can be used with confidence.

There are a number of ways that radiotracer estimation of microbial biomass might be improved. First, even though the vertical diffusion equation seems to work, it would be best to get along without it. In other words, it would be best to use only tracer measurements that reflect full tracer equilibrium, making the diffusion equation unnecessary. One way to hasten vertical equilibrium could be to distribute the tracer vertically throughout the sediment by introducing the tracer through a vertical series of injection portals in the plastic cylinder that holds a sediment core.

Second, it might be possible to bypass the issue of vertical equilibrium by directly measuring the amount of DIC in each vertical segment. The precedure would be as follows: (1) introduce carbon tracer into the sediment core through injection portals at regular vertical intervals; (2) allow several days for the tracer to equilibrate between DIC and particulate fractions; (3) terminate the experiment by freezing and slicing into segments;

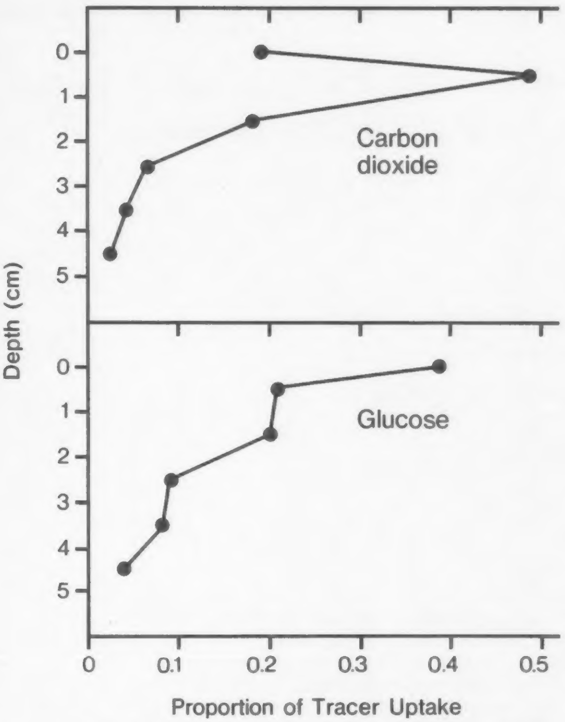

Fig. 6. Vertical distribution of microbial activity, as measured by the uptake of $^{14}CO_2$ and [^{14}C]glucose by sediment microorganisms.

(4) measure the amount of carbon tracer in the DIC and particulate fractions of each segment; (5) directly measure the amount of DIC in each segment by means of infrared gas analysis; (6) estimate the amount of carbon in the living particulate fraction of each vertical segment by using the simple proportion described under Methods. Because of the direct DIC calibration in each vertical segment, estimates of particulate carbon should be valid reflections of the living biomass even if complete vertical equilibrium has not been attained.

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Strontium Labelling for Verifying Daily Growth Increments in the Statolith of the Short-Finned Squid (*Illex illecebrosus*)[1]

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Shrimp soaked in strontium chloride solution were fed to short-finned squid (*Illex illecebrosus*). The strontium was deposited in the statolith of the squid where, with the use of an electron microprobe, it was detectable as a distinct band on the ground surface of the statolith. Strontium X-ray maps and corresponding back-scattered electron images in the atomic contrast mode were obtained. Use was made of a strontium X-ray line profile to discriminate between markings deposited only 2 d apart. Micrographs were compared with light micrographs to verify the daily growth increments.

On a nourri des encornets nordiques (*Illex illecebrosus*) de crevettes trempées dans une solution de chlorure de strontium. Déposé dans le statolithe de l'encornet, le strontium apparaissait comme une bande distincte sur la surface au cours de l'examen à la microsonde électronique. Des tracés de la distribution du strontium ont été obtenus par rayons X ainsi que des images électroniques correspondantes par rétrodiffusion en mode de contraste atomique. On a utilisé un profil du strontium obtenu par rayons X pour différencier les marques déposées à 2 jours d'intervalle. Ces micrographies ont été comparées à des micrographies optiques afin de vérifier l'accroissement quotidien.

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Management of squid fisheries has been hampered by the lack of a valid ageing technique without which such population parameters as mortality rate, growth rate, and recruitment cannot be estimated accurately. For several important commercial squid species, chronological interpretations have been inferred from the comparison of statolith growth increments with modal length frequencies. Rosenberg et al. (1980) and Kristensen (1980) described daily and fortnightly increments in *Todarodes sagittatus* and *Gonatus fabricii*, respectively. Daily and monthly increments have been postulated for *Loligo opalescens* (Brothers et al. 1976; Spratt 1979). Other workers (Lipinski 1978, 1981; Hurley et al. 1979; Hurley and Beck 1979; Morris 1983) found that while increments in younger short-finned squid (*Illex illecebrosus*) conformed closely to a daily interpretation, for older squid the number of rings underestimated the elapsed number of days between samples. In contrast, Radtke (1983), using scanning electron micrographs, found presumed daily increments over all size ranges of the same species.

It might be possible to carry out age verification studies employing laboratory-reared squid. However, many species, including the short-finned squid, are not easily reared from hatching in a laboratory environment.

Dawe (1981) recommended that further age validation studies be aimed at applying a chemical mark on the statolith at a known date. In fish, tetracycline chelates to newly formed calcium carbonate crystals in developing otoliths to form a fluorescent band visible under ultraviolet light (Campana and Neilson 1982; Wild and Foreman 1980). Experience with this technique has been variable. Wild and Foreman (1980) showed the tetracycline fluorescence to be concentrated within one growth increment in the otoliths of yellowfin (*Thunnus albacores*) and skipjack (*Katsuwonus pelamis*) tuna. However, incorporation into the otolith was extended over 14–20 growth increments in flounder, *Platichthys stellatus* (Campana and Neilson 1982), while Kobayashi et al. (1964) noted that dual tetracycline injections remained distinct in goldfish (*Carassius auratus*) only when a month or more was allotted between applications. The precise location of the proximal edge of the band corresponding to the date of injection is often difficult to pinpoint, since the fluorescence is diffuse.

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In this study we chose strontium, rather than tetracycline, as a temporal marker in an attempt to verify the existence of daily growth increments in the statoliths of the short-finned squid. Strontium is well suited for this purpose. It forms a nontoxic divalent cation and has been substituted for calcium in invertebrate statoliths (Spangenberg 1979) and fish scales (Ophel and Judd 1968; Yamada et al. 1979).

Materials and Methods

Squid were obtained on October 20, 1982, from a trap net located in St. Margaret's Bay, near Halifax, Nova Scotia. They were transported to Dalhousie University in Halifax and placed in the pool tank at the Aquatron laboratory, a description of which is given by O'Dor et al. (1977). They were maintained in the tank at a constant increased photoperiod of 16 h light : 8 h dark. The water temperature was kept between 12 and 15°C. Salinity varied from 30.8 to 32.1‰ during the experiment.

Squid to be marked were fed one or two whole, cooked shrimp that had been soaked for 24 h in a solution of 1.2 g strontium chloride·mL distilled water^{-1}. Individual identification of the four squid was made possible by recognition of specific skin abrasion patterns peculiar to each animal. Normal feeding after marking was ad libitum with untreated shrimp.

The squid were kept from 13 to 21 d, i.e. until they died after spawning. They were then sexed, routine body morphometrics were recorded according to Amaratunga and Durward (1978), and statoliths were extracted immediately upon the death of each animal.

Statoliths were extracted by making a single oblique transverse cut through the statocyst exposing the paired statoliths in their maculae. One statolith per squid was chosen at random for analysis, since Lipinski (1981) showed that left and right statoliths gave similar counts of growth increments. It was mounted with the anterolateral (concave) side down on a glass slide in a mounting medium (Protexx). After allowing the mounting medium to harden for 24 h, grinding proceeded using a succession of increasingly finer grit carborundum papers down to 3/0 polishing paper until the ground surface extended to the edge of the statolith along the maximum radius. Each statolith underwent a final polishing with a 1-μm-grit diamond paste.

Statoliths were viewed under bright field with a Zeiss Phot 1 microscope equipped with a 35-mm camera and a drawing arm. The drawing arm was employed to map the outer increments. Normally the outer increments could be seen clearly in light micrographs (Fig. 1A). In cases where certain increments were out of focus on the micrograph and therefore difficult to interpret, the definition of those particular increments was resolved by comparing individual drawing arm maps made by the senior author and a technician. Agreement to within ±1 increment was considered acceptable. The specific identity of each statolith was unknown before the increments were defined. Individual increment widths were measured on the light micrograph with the aid of a graphics tablet and an Apple II E microcomputer.

Strontium in the statoliths was detected by using the JEOL model 35 JXA electron microprobe. The statoliths were examined up to 1 yr after the feeding experiments were completed. Each statolith was mounted on an aluminum stub with 5-min epoxy cement and was carbon-coated. A strontium standard was used to confirm the setting of the wavelength dispersive X-ray spectrometer at the strontium X-ray wavelength. A strontium X-ray map of each statolith was obtained (Fig. 1B) together with a photograph of the back-scattered electron image (Fig. 1C). A bright band, corresponding to the strontium X-ray band, is seen in the back-scattered electron image in the compositional or atomic contrast mode. A strontium X-ray line profile across the statolith (Fig. 1D) produced a quantitative image of the changes in strontium X-ray activity along the scanned line which was used to pinpoint the site of first incorporation of the strontium and to discriminate between closely spaced labels (Fig. 2).

Attempts to enhance the increments by acid etching after strontium analysis were not successful. Our own experience in acid etching statolith increments and illustrative evidence found in Radtke (1983) suggest that only a thin band of crystals whose long axis parallels the ground surface of the statolith are etchable. Since this band is thinnest near the edge of the statolith, it may be that repolishing to remove the carbon coating obliterated these "etchable" crystals.

Age validation counts of increments for each statolith were made by projecting the X-ray line profile/back-scattered image (Fig. 1D) on its respective light micrograph and counting the number of increments along the maximum radius from the proximal edge of the strontium band to the outer edge of the statolith. Use of the X-ray line profile was preferred to the X-ray map, since the site of first incorporation of the strontium could be located consistently to within less than 1 μm in trials with independent observers. Since the increments had been defined previously, this ensured a high degree of accuracy in counting increments.

Results and Discussion

Four statoliths from one male and three female mature squid were analyzed for strontium. The morphometric and age validation information for these squid is summarized in Table 1. Overall there was good agreement over the period between the number of increments and the time elapsed in days. Individual differences which ranged from 0 to (−) 3 increments indicated that certain increments were not included in some counts. Differences from the expected value may have resulted from not seeing very faint increments. The rather high standard deviation of the mean increment width for one statolith (marked on November 13) which differs the most from the number of days elapsed supports this hypothesis.

One squid that was fed strontium twice, 2 d apart, showed a double strontium peak (Fig. 2) in its statolith. The distance between the two peaks was approximately 3 μm. This conforms closely with the mean increment width of 1.7 μm for the statolith (Table 1). This is indirect evidence that the strontium appeared in the statolith within 24 h of its application. The range of average increment widths (1.7–2.8 μm) for the four statoliths in this study is similar to that of field specimens (2.0–2.6 μm) over the November period (Morris 1983). The general appearance of the increments on the "laboratory" and the "wild" side of the strontium mark appears to be similar (Fig. 1A).

These results have demonstrated the feasibility of using strontium as a chronological marker for labelling squid statoliths. The permanent strontium band could be detected by means of either the X-ray map or the back-scattered electron image. However, the strontium X-ray line profile located the site of first

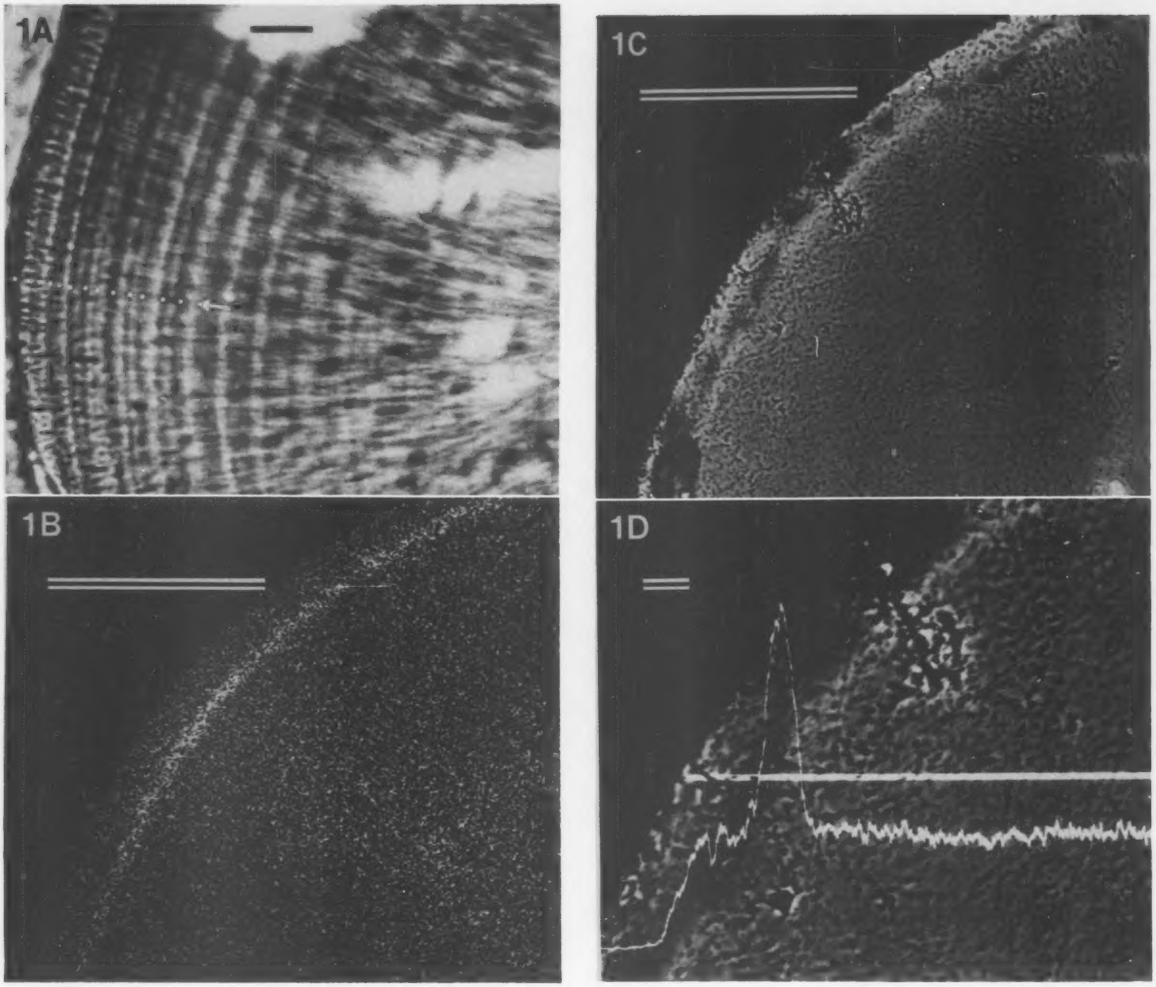

FIG. 1. Micrographs of ground statolith from squid (marked on December 1, 1982) showing various techniques for detecting strontium and its use in age validation. (A) Light photomicrograph. The 13 growth increments are indicated on the photo. Arrow indicates increment produced on date of feeding strontium. Bar = 10 μm. (B) Strontium X-ray map of statolith. Strontium band shows up as band of dots indicative of high level of strontium X-rays. Bar = 100 μm. (C) Back-scattered electron image. Bright line, corresponding to strontium X-ray band, indicates presence of strontium. Bar = 100 μm. (D) X-ray line profile superimposed on back-scattered electron image. Strontium X-ray peak corresponds to bright strontium band in back-scattered image. Bar = 10 μm.

TABLE 1. Summary of squid morphometrics and age validation information for statoliths marked with strontium.

Date marked marked	Date squid died	Sex	Mantle length (mm)	Time elapsed (d)	No. of increments	Average ± SD increment width (μm)
Nov. 13, 1982	Nov. 27, 1982	M	220	14	11	2.8±0.3
Dec. 1, 1982	Dec. 13, 1982	F	248	13	13	2.3±0.1
Nov. 17, 1982	Dec. 4, 1982	F	247	17	17	2.2±0.1
Marked twice: Nov. 13 and 15, 1982	Dec. 4, 1982	F	240	21, 19	20, 18	1.7±0.1

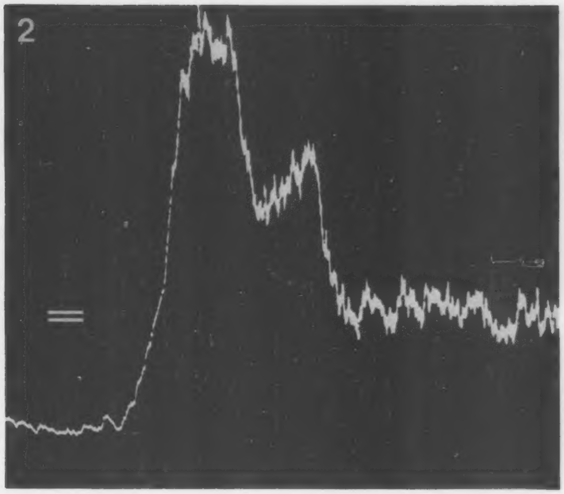

FIG. 2. X-ray line profile showing double strontium peak corresponding to two feedings (November 13 and 15, respectively). Bar = 1 μm.

incorporation of a strontium marker more precisely than the other two techniques and provided the best spatial discrimination of sequentially deposited strontium bands. In this regard, strontium may be a better marker than tetracycline in age validation studies.

Nonvalidation of daily increment formation in older short-finned squid by modal analysis of length frequencies reported in earlier studies is probably due to the presence of mixed age groups in the samples (Dawe 1981; Hurley et al. 1979).

Since the composition of squid statoliths is similar to that of fish otoliths (Hurley et al. 1979; Radtke, 1983; Degens et al. 1969), there is good reason to believe that strontium labelling of fish otoliths may be feasible.

In previous experiments (P. H. Odense and V. Logan, pers. comm.) it was not possible to detect strontium in the scales of salmon (*Salmo salar*) fed strontium chloride in gelatin pellets. With the improved X-ray detector sensitivities now available it may be feasible to label fish scales and otoliths with strontium and other elements, and to employ these techniques in fisheries management either in chemoprinting or ageing studies.

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Influence of Light on the Alkaline Phosphatase Activity of *Selenastrum capricornutum* (Chlorophyceae) in Streams

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Klotz, R. L. 1985. Influence of light on the alkaline phosphatase activity of *Selenastrum capricornutum* (Chlorophyceae) in streams. Can. J. Fish. Aquat. Sci. 42: 384–388.

The alkaline phosphatase activity (APA) of *Selenastrum capricornutum* Printz incubated in situ in four streams in New York State was inversely related to total insolation. APA was not correlated with stream molybdate reactive phosphorus over the range of concentrations encountered. *Selenastrum* showed no diel cycle of APA. The phosphorus fraction made available by the activity of alkaline phosphatases, enzyme hydrolyzable phosphorus (measured for the first time in streams), increased the phosphorus supply to organisms with high APA.

L'activité de la phosphatase alcaline (APA) de *Selenastrum capricornutum* Printz incubée in situ dans quatre cours d'eau de l'état de New York était en rapport inverse à ensoleillement total. L'APA n'était pas en corrélation avec les concentrations de phosphore réactif au molybdate présentes dans les cours d'eau. *Selenastrum* n'a pas exhibé de cycle nycthéméral de l'APA. L'apport de phosphore aux organismes possédant une APA élevée a augmenté par suite de l'activité des phosphatases alcalines, enzymes capables d'hydrolyser le phosphore, qui ont été quantifiées pour la première fois dans un cours d'eau.

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Despite the abundance of data on the effects of phosphorus on algae in lakes, relatively little is known about factors regulating the nutrient's effects in rivers (Elwood et al. 1981; Peterson et al. 1983). Flowing water can provide a continuous supply of P to epilithic stream organisms, at a rate controlled by the rate of diffusion through a laminar flow boundary layer around the cells (Whitford 1960). Water velocity and water column P concentration influence the diffusion rate and therefore the availability of P to these organisms. Increased water velocity ($0-18\ \mathrm{cm \cdot s^{-1}}$) resulted in increases in P uptake by filamentous algae up to 43-fold, as well as higher respiratory rates (Whitford 1960; Whitford and Schumacher 1961, 1964; Schumacher and Whitford 1965). Sperling and Grunewald (1969) and Lock and John (1979) also found that water flow increased P uptake by river periphyton in laboratory studies. High phosphate concentration negated any effect of water movement on P uptake by periphyton over a range of velocities (Lock and John 1979), presumably because the P demand of the microorganisms was satisfied by molecular diffusion across the boundary layer at the high phosphate concentration. There is some indication that the N/P ratio of the stream water may be the factor determining P limitation, not just the available P concentration (Moller et al. 1975; Healey and Hendzel 1980).

Algae respond to limiting inorganic P conditions by producing alkaline phosphatases which cleave inorganic phosphate groups from certain organic P compounds, making them available to the algae. This enzyme hydrolyzable phosphate (EHP, Strickland and Parsons 1968) may be important to algae that are limited by inorganic P in the marine (Taft et al. 1977) and lacustrine environments (Berman 1970; Heath and Cooke 1975; Francko and Heath 1979; Petterson 1980; Wynne and Berman 1980; and Wetzel 1981), but it has not been studied in streams. High alkaline phosphatase activity (APA) does not necessarily indicate P limitation, for there may be sufficient EHP in the water for the algae.

The present study was conducted to determine the factors controlling algal APA under stream conditions. *Selenastrum capricornutum*, originally isolated from a river, was incubated in dialysis chambers in situ in four streams in central New York State and analyzed for APA and growth rate.

Materials and Methods

The four streams studied in Cortland County, New York State, were chosen to provide a range in habitats and stream water chemistry (Table 1). Two of the streams (sites 1 and 3) drained predominantly agricultural watersheds (Table 2); two (sites 2 and 4) drained predominantly wooded watersheds. Site 1, Gridley Creek, received complete solar exposure; site 2, a tributary to Gridley Creek draining Woodchuck Hill, was shaded part of the day; site 3, Hunts Creek, had a nearly complete canopy of Willow; and site 4, Hoxie's Gorge Creek, was totally shaded due to a complete tree canopy and gorge.

Selenastrum capricornutum Printz, the United States standard algal assay organism originally isolated from the River Nitelva, Norway, was incubated at the four sites for 7-d periods during the spring, summer, and fall of 1982. Six days before

TABLE 1. Means (SD) of water quality parameters (measured in 1980–81).

Parameter	Site 1	Site 2	Site 3	Site 4
Conductivity (μS)	198 (203)	70 (42)	103 (59)	77 (38)
NO$_3$–N (mg·L^{-1})	0.907 (0.530)	0.108 (0.085)	1.494 (0.653)	0.441 (0.161)
Ca (mg·L^{-1})	32.2 (14.2)	17.2 (8.24)	26.2 (5.52)	18.1 (5.70)
K (mg·L^{-1})	1.47 (0.53)	0.65 (0.20)	1.29 (0.43)	0.69 (0.22)
Mg (mg·L^{-1})	5.82 (2.49)	3.21 (1.42)	3.83 (1.14)	2.94 (1.06)
Na (mg·L^{-1})	No data	1.58 (1.44)	2.08 (0.74)	1.32 (0.62)

TABLE 2. Characteristics of the four streams and watersheds.

	Site 1	Site 2	Site 3	Site 4
Land use (%)				
Agricultural	94.9	2.0	96.5	1.9
Wooded	5.1	98.0	3.5	94.2
Abandoned field	0	0	0	3.9
Watershed area (km^2)	49.2	18.8	16.5	17.6
Elevation at site (m)	413	407	389	398
Stream characteristics				
Total length (km)	13.1	2.86	3.89	4.24
Order	2nd	1st	1st	1st
Discharge (m^3·s^{-1}) mean (SD)	1.79 (5.70)	0.38 (1.18)	0.34 (1.09)	0.10 (0.23)
Soil type[a]	16% VHL 42% LVM 42% VML	100% LVM	50% LVM 50% VML	7% VML 93% LVM

[a]VHL, Valois-Howard-Langford; LVM, Lordstown-Volusia-Mardin; VML, Volusia-Mardin-Lordstown.

a field test, the algal cells were inoculated into 50 mL of low-nutrient 3.6 medium (Klotz et al. 1975) in a 250-mL Erlenmeyer flask for a final concentration of approximately 10^5 cells·mL^{-1}. The cultures were grown at 4300 lx with a 16 h light : 8 h dark cycle. On 4 and 2 d prior to the field incubation, 50 mL of 3.6 medium was added to each of the cultures. At the start of the field incubation, the cells were concentrated by pouring the supernatant and inoculated into the dialysis chambers to give a final count of approximately 10^7 cells·sack^{-1}.

Dialysis chambers of 2.7-cm-diameter dialysis tubing (VWR Scientific, molecular weight cutoff: 12 000 – 14 000) were prepared by soaking and rinsing strips of tubing in distilled water, securely knotting one end, and filling the tubes with 40 mL of 3.6 medium. A cotton-stoppered section of glass tubing was inserted into the open end of each dialysis chamber and tied securely in place. Chambers were then immersed in 3.6 medium in a cotton-stoppered flask and sterilized by autoclaving for 20 min at 121°C and 1.02 atmospheres (103.352 kPa). The algae were inoculated into the chambers by breaking the tubing over a flame and pipetting in the algae. The dialysis tubing was then knotted below the glass tubing and tied and excess material removed. Typically, three chambers were held in place in each stream by tying them to wooden stakes.

After incubation, dialysis chambers were brought back to the laboratory, the cells counted using a hemacytometer, the volume of water in the chambers measured, and the cells harvested by centrifugation. Growth rates were expressed as population doublings per day. Prior to centrifugation the culture was divided in two to allow for a blank in the determination of APA.

The APA of the harvested cells was determined by a modification of the techniques of Fitzgerald and Nelson (1966) and Sayler et al. (1979). The algal cells were washed with 3.6 medium lacking P to remove any extracellular P that might influence the APA determination. Three millilitres of 1 mol Tris buffer·L^{-1} (pH 8.6) was added to the algal pellet in each centrifuge tube, followed by 1 mL of *p*-nitrophenylphosphate solution (*p*-NPP, Sigma; 1 mg·mL^{-1} in 1 mol Tris buffer·L^{-1}, pH 8.6). Blanks received 1 mL of Tris buffer at pH 8.6 without *p*-NPP. Alkaline phosphatases cleave phosphate groups from *p*-NPP, producing *p*-nitrophenol (*p*-NP), a compound that can be quantitatively measured colorimetrically. Following thorough mixing with a vortex mixer, the algal cells were incubated at 37°C in a waterbath for approximately 2 h. The reaction was stopped by adding 1 mL of 1 mol NaOH·L^{-1} to each tube, the cells removed by centrifugation, and the supernatant measured at 418 nm with a Spectronic 70 spectrophotometer. *p*-NP production was compared with a standard curve, and specific APA was expressed as nanomoles of P hydrolyzed per 10^7 cells per hour.

To test the relationship between light intensity and APA under controlled conditions, dialysis chambers were incubated in sun and shade river reaches at both sites 1 and 3. In both rivers, the shaded location was located in a similar flow regime

TABLE 3. Alkaline phosphatase activity (APA) (nmol P hydrolyzed · 10^{-7} cells · h^{-1}) and doublings per day of *Selenastrum* incubated in situ in dialysis chambers at the four sites.

Site	Mean	SD	*n*	Mean doublings per day	SD
1 Agricultural	0.27	0.10	7	0.60	0.36
2 Wooded	0.73	0.99	9	0.54	0.29
3 Agricultural	0.99	0.70	10	0.47	0.35
4 Wooded	2.55	2.06	8	0.28	0.28

just 10 m upstream from the sun location, thus controlling all variables except total insolation. At site 1 the sun site was the regular site used for the biweekly analyses (Table 3); at site 3 the shade site was the regular site.

The diel cycle of APA in *Selenastrum* was determined in laboratory cultures in duplicate 500-mL flasks under a 12 h light : 12 h dark cycle. Cells were cultured under two regimes: in 3.6 medium for 2 wk, and in 3.6 medium for 2 wk followed by 2 wk in 3.6 medium lacking P. Under both regimes 100 mL of fresh medium was added every 2 d after decanting 100 mL of old medium.

Molybdate reactive phosphorus (MRP) analyses were performed on unfiltered river water samples the day of collection by the ascorbic acid method (American Public Health Association et al. 1975). Prefiltered (0.45-μm Millipore HA) stream water from the four sites was analyzed on six dates from May to September 1984 for various P fractions. EHP, that P fraction made available to organisms with alkaline phosphatases, was determined by the method of Strickland and Parsons (1968), total P was determined by persulfate digestion followed by the ascorbic acid method (American Public Health Association et al. 1975), and soluble reactive phosphorus (SRP) was determined by the ascorbic acid method. Nitrate was analyzed by the Cd reduction method (American Public Health Association et al. 1975) on the day of collection; colorimetric analyses were made with a Carey recording spectrophotometer. Ca, K, Mg, and Na concentrations were determined with a Perkin Elmer model 303 atomic absorption spectrophotometer.

Results

Selenastrum APA increased with the degree of shading at the four sites during 1982. *Selenastrum* grown at wooded site 4 had the highest APA, followed by algae cultured at agricultural site 3, wooded site 2, and agricultural site 1 (Table 3). The four sites differed significantly in APA (ANOVA, $p = 0.005$); the Student–Newman–Keuls procedure at the 0.05 level revealed that site 4 differed from sites 1–3. The mean growth rates as population doublings per day of the algae decreased from site 1 to site 4 (Table 3). However, when the relationship between APA and growth rate was analyzed by the Pearson product moment correlation procedure (Nie et al. 1975) there was no significant correlation, either by site or with all sites grouped together.

The four sites differed in terms of the MRP concentration of the water column (Table 4), and the differences were unrelated to watershed type. Site 1 had the highest mean annual MRP, followed by site 4, 3, and 2. No significant correlation existed between MRP and APA, either by site or with all sites grouped together. Indeed, site 4 with the highest APA had the second highest mean annual P concentration. EHP at the four sites increased the P availability at high APA (Fig. 1). Comparison of SRP and EHP with total soluble P indicated that some soluble P in stream water is not available through the activity of alkaline phosphatases.

TABLE 4. Molybdate reactive phosphorus (MRP) concentrations (μg P · L^{-1}) of stream water at the four sites.

Site	Mean	SD	*n*	Significantly different than sites[a]
1 Agricultural	10.5	8.1	16	2 (0.002), 3 (0.032)
2 Wooded	4.1	3.9	19	1 (0.002), 3 (0.014), 4 (0.000)
3 Agricultural	6.0	5.3	19	1 (0.032), 2 (0.014), 4 (0.001)
4 Wooded	9.6	5.6	19	2 (0.000), 3 (0.001)

[a] *t*-test for paired data, *F*-test determined variances from same population. Log_n transformation for site 1 with 2. Significance level in parentheses.

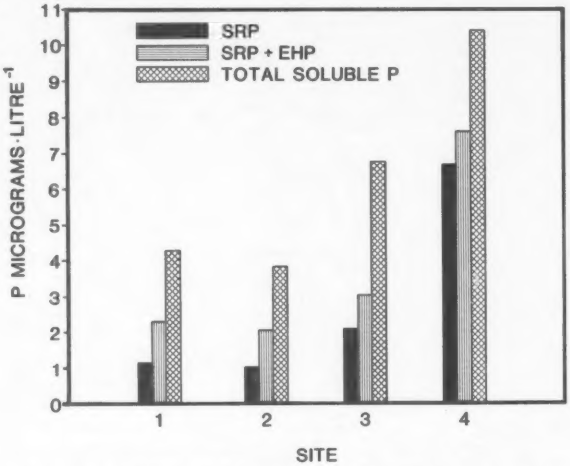

FIG. 1. Soluble reactive phosphorus (SRP), enzyme hydrolyzable phosphorus (EHP) + SRP, and total soluble P for six dates, May–September 1984. Standard deviations (SRP, SRP + EHP, total soluble P): site 1 (0.68, 0.65, 1.38), site 2 (0.57, 0.25, 2.33), site 3 (1.22, 0.72, 2.62), site 4 (2.42, 2.36, 3.07).

TABLE 5. Alkaline phosphatase activity (APA) (nmol P hydrolyzed · 10^{-7} cells · h^{-1}) and doublings per day of *Selenastrum* incubated in situ in dialysis chambers at sun and shade locations at sites 1 and 3.

Site	Light intensity (μEinsteins · m^{-2} · s^{-1})	APA	Doublings per day
1 Sun	1620	0.35±0.10	0.57±0.03
1 Shade	13.5	5.29±0.92	0.38±0.03
3 Sun	1590	0.33±0.01	0.59±0.01
3 Shade	630	1.13±0.15	0.58±0.01

APA was inversely related to total insolation when measured under controlled conditions in the same stream reach (Table 5). With greater than a 100-fold difference in light intensity at the two locations at site 1, there was a greater difference in APA (0.35 vs. 5.29) between the sun and shade sites than at site 3 (0.33 vs. 1.13) with less than a threefold difference in light intensity. There was a decrease in the growth rate in the shade

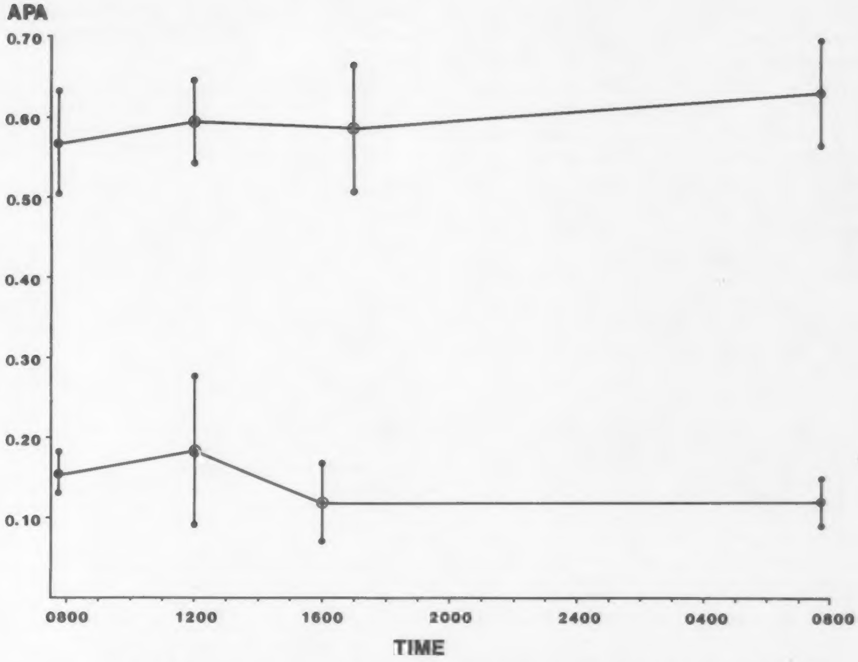

FIG. 2. Diel alkaline phosphatase activity (APA) of *Selenastrum* under a 12 h light : 12 h dark cycle (lights on at 08:00). Open circles designate measurements made during the light period; closed circles designate measurements made during dark period. Upper line represents cells grown in 3.6 medium without P; lower line represents cells grown in 3.6 medium with P. Vertical lines represent standard error.

location at site 1 compared with the sun (0.38 vs. 0.57), but at the site 3 locations there was no significant difference. *Selenastrum* showed no diel cycle in APA under either P replete or limiting conditions (Fig. 2).

Discussion

Selenastrum APA was regulated by the total insolation reaching the stream; elevated APA was measured at more shaded locations (Tables 3 and 5) and was not correlated with MRP of the water column. The sites with the lowest SRP (Fig. 1) had the lowest APA (Table 3). Others have shown that phosphatase is induced or derepressed in algae by growth-limiting orthophosphate concentrations (Kuenzler and Perras 1965; Lien and Knutsen 1973; Aaronson and Patni 1976; Rivkin and Swift 1979). However, the lack of an inverse relationship between APA and ambient inorganic P has been noted previously, and has been linked to internal P reserves or to rapid turnover of ambient P (Fitzgerald and Nelson 1966; Perry 1972; Wynne 1977). Also, Moller et al. (1975) found that the N/P ratio of the external medium influenced APA.

Rivkin and Swift (1979) found that APA in the marine dinoflagellate *Pyrocystis noctiluca* seemed to have an indirect dependence on light; however, the response was the opposite of the response of *Selenastrum* noted here. *Pyrocystis* showed increased APA in the light, a pattern that was internally controlled. Studies using metabolic inhibitors indicated that a reduction of oxidative metabolism was perhaps responsible for reduced APA (Rivkin and Swift 1979). The diel pattern of increased APA during daylight hours found for *Pyrocystis* is not universal. Perry (1976) found no detectable rhythm in the diatom *Thalassiosira pseudonana* and no detectable rhythm was found for *Selenastrum* in this study (Fig. 2). The differences in temporal variations in APA noted in algae may be a factor in the cooccurrence of species in a phosphate-poor environment, with the EHP fraction made available to different species at different times of the day.

If APA can be considered a good measure of P limitation (Nalewajko and Lean 1980), then the mechanism responsible for increased APA under low light intensity may be linked to P uptake, which is an energy-dependent reaction (Blum 1966; Healey 1973). Photosynthesis or respiration may supply the energy for phosphate uptake in algae (Nalewajko and Lean 1980). Healey (1973) showed that phosphate uptake may be stimulated by light, with saturation occurring at low light intensities. Decreased phosphate uptake due to the greatly reduced light intensities under shaded stream conditions may stimulate alkaline phosphatase production, thus increasing the pool of P compounds potentially available to the algae. The EHP of stream water, measured for the first time in this study, increased P supply (Fig. 1). Data from sun and shade locations at site 3 (Table 5) indicate that the P potentially made available by the production of alkaline phosphatases (Fig. 1) may have maintained the growth rates of the alga under conditions limiting phosphate uptake; APA was 3-fold higher in the shade, while the doublings per day remained essentially equal. The linking of phosphate uptake to light intensity agrees with other studies showing light to regulate nitrate uptake in northern California (Triska et al. 1983) and Oregon (Gregory 1980) streams.

The use of dialysis chambers eliminates certain problems in the interpretation of APA data for algae. Others have shown that senescent cells may have high APA regardless of ambient inorganic P concentrations (Grusky and Aaronson 1969). Since natural populations of algae may vary in APA due to the age of the cells, they would not accurately reflect the inorganic P availability. This would be particularly true in streams during an extended period between spates, a situation allowing a buildup of older cells in the periphyton community. Also, certain organisms will maintain high APA once it is induced regardless of the current ambient P supply. Dialysis chambers started with a uniformly grown fresh inoculum measure the APA of the algae under the environmental conditions at the time. Dialysis chambers also allow determination of APA production of a single species rather than a periphyton assemblage composed of many species, each possibly responding in a different manner.

Acknowledgements

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PERSPECTIVES

The Human Factor in Fishery Resource Management

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Scientists working within a geographic area require a forum where the scientific basis of resource management plans can be vetted. Good science then only becomes good management if the management plan or regulations are accepted by fishermen. Scientists and managers frequently assume that fishermen oppose resource management when the latter disregards a management plan developed without consultation or presented in an unclear manner. I show that certain eastern Canadian and Californian inshore fishermen have a positive concern for resource management, and that management plans can be successfully developed within a consultative process. Scientists and managers must present new concepts and resource-based science to their clients (the fishermen) in a lucid fashion. Once a mutual understanding is developed, good resource management can follow.

Les scientifiques travaillant dans un secteur géographique donné ont besoin d'un cadre dans lequel la base scientifique des plans de gestion des ressources peut être examinée de près. De bonnes données scientifiques se traduisent par de bonnes méthodes de gestion seulement si le plan de gestion ou les règlements sont acceptés par les pêcheurs. Les scientifiques et les gestionnaires présument souvent que les pêcheurs s'opposent à la gestion des ressources lorsque ceux-ci ne tiennent pas compte d'un plan de gestion qui a été élaboré sans consultation ou présenté d'une façon qui n'est pas claire. Je démontre que certains pêcheurs côtiers de l'est du Canada et de la Californie s'intéressent de façon positive à la gestion des ressources et que les plans de gestion peuvent être élaborés avec succès dans le cadre d'un processus de consultation. Les scientifiques et les gestionnaires doivent présenter à leurs clients (les pêcheurs) de nouveaux concepts et des informations scientifiques basées sur les ressources d'une façon qui soit compréhensible. Une fois que la compréhension se sera établie de part et d'autre, de bonnes méthodes de gestion des ressources pourront être appliquées.

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Cushing (1974) pointed out an important relationship between science and resource management. He concluded that successful science promotes successful management when all else is equal. Rarely must the latter have been the case, as there is more good science than fisheries management success stories. Walker (1973) contended that there is a basic flaw in scientific management: "… it is founded on an understanding of the natural system and not the human system." It has been my experience in fishery science that scientist – resource manager – fisherman relations are a variable in the resource management equation that is often ignored. If little confidence exists between these parties, the best of management plans will fail. Whether the system employed by the regulatory body is democratic or authoritarian makes little difference. Fishermen under the former may vote against a good plan; fishermen under the latter may disregard it (enforcement is not cost-effective where the majority disregard regulations).

Thus, the human aspects must be considered; to permit good science to become good management, scientists, resource managers, and fishermen must communicate effectively. Unfortunately, all too frequently there is mistrust on both sides. My experience has been that many scientists and managers feel that fishermen have little concern for either the resource base or the future of the fishery. This attitude clouds their objectivity and influences their approach to fishermen, which ultimately results in confrontation between government and industry. I present evidence here that many bona fide coastal fishermen are concerned about their resource and will work toward conservation if approached in a positive manner and permitted to have input into management plans.

Canadian Fishery Regulation Development: Background

Renewable marine resources in Canada are a "common property resource" under federal government jurisdiction (Weeks and Mazany 1983), as they belong to the people of Canada, not to any individual group, including commercial fishermen. (I have yet to hear this fact presented to fishermen, and most of the latter are unaware of it. They believe the resource they prosecute is theirs to do with as they feel.) Thus, fishermen are given the privilege to fish on behalf of the Canadian people. It follows that fishing activities should then be carried out in a manner that benefits society as a whole. The federal government decided years ago that a fishery conservation scheme was required. The model chosen by government personnel to best accomplish this is akin to Larkin's (1977) techno-centric model in which harvest rates by species, area, season, gear type, etc., are controlled by the state. Controls are laid out for each species as regulations under the Fisheries Act.

Regulations in the past were often developed unilaterally by civil servants employing professionally developed biological and economic concepts as rationale. The Department of Fisheries and Oceans employs fishery officers in each district — the focal point for department–fishermen interactions. Their primary role has been enforcement of the Fisheries Act. They frequently delivered to their local industry tidings of new regulations. Often this was the first time fishermen were informed of regulations constricting their ability to prosecute the fishery. Their reaction would be bitter to the news that their season was shortened, their favorite fishing site closed, or their right to prosecute a fishery lost. The officer was usually not equipped to respond satisfactorily to the barrage of departmental criticism following such announcements. (Miller (1976) suggested that the rationale for each new regulation be handed out to fishermen so they may better understand the benefit to the fishery.) The fishermen's reaction could be interpreted as a lack of concern for either their future, the resource, or both. The fishermen, if extremely concerned, might successfully harangue government and/or parliamentary members; a meeting might then be arranged where headquarters or regional staff were expected to interpret the new regulation(s). Meetings frequently occurred in smoke-filled halls, on cold winter evenings. The fishermen, after the fact, rarely wanted to listen to logic, particularly from strangers. This could be the departmental members' first contact with these fishermen. Little wonder the former might come away from such an encounter feeling that indeed fishermen are opposed to conservation and that they only care about today and not tomorrow.

My experience has been that scientists and managers rarely look at the system of fishery resource management and its product, from the fishermen's perspective. Careful inspection would disclose that (1) the bulk of the regulatory decisions in the past have been made by nonfishermen and (2) in spite of regulations, many of our stocks have not been well managed. Thus, cynicism of the system and government personnel by fishermen is common.

The Honourable Romeo LeBlanc, from a coastal Maritime riding, was appointed Secretary of State for Fisheries in the early 1970's and, later, Minister of Fisheries. He decreed that there would now be consultation with fishermen before decision making. I was hired in 1974 to develop a program that would provide the biological data necessary to permit management of the Maritime marine plant resource (Pringle 1976). This position carried with it the responsibility for the "Marine Plants Experimental Station" located in western Prince Edward Island at Miminegash, the self-proclaimed "World's capital of Irish moss." The fishermen here prosecute a number of fisheries, from lobster to herring, but Irish moss is the most important economically. I chose to live with my family in the village for six field seasons. The experience was invaluable. Much was learned by both sides. My most important lesson was that the bulk of fishermen care about the resource base and, given an informed choice, will come down on the side of conservation. The following examples illustrate this point.

Examples Demonstrating that Fishermen Care

Maritime Inshore Fishery

My first assignment was to develop marine plant regulations "in consultation" with industry. A series of meetings was scheduled in local marine plant harvesting communities where the proposed regulations could be jointly discussed. The meetings were organized and presided over by an official of the local fishermen's association. The marine plant harvest in many of the communities visited was sufficiently insignificant that the concept of regulations was of little concern to the majority of harvesters. This made the development of local statutes relatively easy. Where the fishery played a significant economic role the meetings were well attended and the debate lively.

Chondrus crispus Stackhouse (Irish moss) is a significant fishery off western Prince Edward Island (Ffrench 1971). The center of the fishery is Miminegash. Here, decision to introduce resource management concerned harvesters sufficiently to organize an in camera meeting prior to our scheduled meeting. An overwhelming majority voted in favour of maintaining the status quo. The local fishery officer advised me that further debate would be fruitless. Given the departmental policy it would be untenable to bring down regulations without at least an attempt at conciliation. The scheduled meeting was held.

I prepared and delivered a presentation that attempted to justify fishery resource management in general, and marine plant regulations in particular. The concept of a "common property resource" was outlined as was the usual fate of such resources where unregulated exploitation was permitted. The federal government's jurisdiction over marine natural resources was noted; a number of stock collapses were discussed. I claimed that as the federal government is the steward of the resources, it must be held responsible for overexploitation. The government's stated aim, to reverse past trends in fishery exploitation, was discussed as was its objective to maximize returns to all sectors.

The harvesters agreed that certain local fishery stocks had collapsed and that regulation of fisheries by an external agency was required. (They noted that they had attempted to manage the Irish moss resource themselves but to no avail.) However, it was obvious they had been affronted for years by government dictating regulations for "their" fishery.

The discussion revealed that all was not well with the Irish moss fishery: their once "unlimited" Irish moss beds were not yielding as they had and they were concerned; farmers, school teachers, and vacationers were exploiting their fishery; gear technology was under debate; etc. Could we resolve these problems and others? By the evening's end an unanimous vote was recorded in favor of the concept of regulations. Since the formation of these regulations, amendments have been made through consultation: seasons shortened, licenses limited, and gear restricted.

Irish moss is cropped in the southern Gulf of St. Lawrence by towing dragrakes behind lobster boats; the fronds bind between the tines (Scarratt 1972; Pringle 1979). A certain percentage of the fronds removed from the bed are not captured. Harvesters developed the basket dragrake (wire mesh behind and above the tines) to trap these unattached fronds. The buyers claimed that the crop from basket dragrakes, as opposed to the dragrakes, contained excessive amounts of sand, gravel, and rock. They had attempted in vain to discourage their use. Certain harvesters claimed that the increased efficiency provided by the basket dragrake was an economic necessity. One of the harvesters' chief concerns with regulation implementation was the government's possible unilateral use of them to ban harvesting gear. I had suggested that harvesting gear would not be banned without a demonstration of adverse ecological impact.

The concern about the possibility of severe, adverse ecological impact by harvesting gear was sizeable. Consequently, a 2-yr study was designed and initiated. The first year's data were presented to the harvesters (Pringle 1979; Pringle and Sharp 1980); the impact on both lobsters and Irish moss was significant. The harvesters did not want another year's data. They voted that evening to ban the basket dragrake.

A committee of harvesters and government personnel was struck to design and test a suitable replacement for the banned basket dragrake. One of the three prototypes tested had acceptable fishing power and a significantly less adverse ecological impact (Pringle et al. 1979). When the data were presented to the harvesters, they voted against use of the new basket. They felt the employment of any type of basket might lead to surreptitious use of the banned basket dragrake.

I was dumbfounded; we had a success story (rare in fisheries science) and the harvesters prevented us from enjoying it. Their concern was clear; they would rather be somewhat inefficient than increase the adverse ecological impact on their two main commercial species, lobster and Irish moss.

Like most fisheries on Canada's east coast, the fishing pressure on the Irish moss beds in District 1 (Miminegash area) was excessive (Pringle and Semple 1984). When the regulations were enacted, federal legislation dictated that all harvesters showing evidence of harvesting Irish moss in any 1 yr of the previous 3 yr were eligible for a license. The mean annual landings had declined from 12 000 t (1966–71) to 8 000 t (1972–79). Resource abundance appeared to be the problem (Pringle 1981). The Gulf of St. Lawrence Marine Plant Advisory Committee (industry and government representatives) failed to develop an adequate solution to this problem. There was not a fisherman in the district that could now afford to foresake "mossing." Many had begun harvesting during the development period of a decade earlier (Pringle 1981) and had become dependent on the harvest for a good proportion of their annual incomes, particularly when the subsidy of unemployment insurance was included. (Fishermen received weekly credit toward unemployment insurance (UI) benefits. Where unemployment in a region is greater than about 20%, one can receive benefits for 42 wk, having worked only 8–10 wk.)

The outlook for the 1978 season was not good. The 1977 CPUE was low and our preseason (1978) biomass assessment suggested another poor crop. The fishermen, when so informed, agreed that harvesting should not take place. The spring herring season had been poor, however, and monies were required to get them through to the lobster season (2 mo). An appeal to extend UI benefits was turned down: thus, the harvesters reluctantly went mossing.

The action of the harvesters, from a distance, might appear as if they had little concern for the resource; the alternative for most was welfare. Feeling that more resource knowledge would help to prevent a reoccurrence of this plight, the harvesters, at this bleak time, voted to turn over one of their smaller beds (Horses Head, see Pringle and Semple 1983) as a research experimental site — a gesture in keeping with their concern for the resource.

Examples from the Eastern Pacific

Recent discussions with certain American government fishery pesonnel confirmed my contention that scientists and managers frequently feel that fishermen are opposed to conservation. One respected scientist presented the pillage of the California sardine (*Sardinops sagax* (Jenyns)) stocks in the 1930's and 1940's as an example of fishermen abusing their resource. A paper was referred to me, written by a late fishery biologist with the California Division of Fish and Game (Radovich 1981), in which the stock collapse was traced. Radovich correctly pointed out that warnings of an impending collapse were ignored "... by the fishing industry which was able to identify scientists who would state ... that it was virtually impossible to overfish a pelagic species." Radovich employed the collective term "industry," which includes both processors and fishermen. Did he mean both, or mainly the former? I would argue that the behaviour and attitudes of each toward the resource are distinguishable. This is no doubt due to distinctly different backgrounds and sources of future incomes.

Processors frequently are investors from outside the fishing community, often from across the continent (McEvoy 1979) or from a foreign country. Consequently, they tend not to be as dependent as fishermen on local stocks for future income. For example, the pioneer salmon canners of California, following the collapse of the salmon fishery, turned to sardine canning (McEvoy 1979). These processors then moved to Peru to process anchovies following the California sardine stock collapse. Once the Peruvian fishery collapsed the companies moved to Mexico. I witnessed a similar movement by Canadian herring processors in the late 1960's: following the collapse of the Pacific coast fishery, west coast companies invested in the Maritime herring industry.

Although processors no doubt prefer to see healthy stocks, I suggest that they do not have the same long-term outlook as fishermen. This is evident from remarks by California State fishery biologists. Clarke (1982) noted "The processors, the reduction people were vociferous in their resistance to the California Department of Fish and Game's attempt to hold down the catch ... The processors were certainly far from polite in the things they said to us. ..." Croker (1982) noted that an influential government biologist at the State Capitol "... couldn't buck the big canning industry ... Some people were genuinely concerned, but many in the industry refused to worry. They were making big money and couldn't care less about the future."

In contrast with the processors, bona fide coastal fishermen are more insular. First, fishing tends to be carried on from generation to generation. They tend to begin their vocation at an early age and most must fish to maintain economic independence (fishing, frequently, is their only vocation). They are often dependent on local fish stocks for their livelihood. They generally have either witnessed stock collapses which they feel were caused by overexploitation or have heard anecdotal evidence of the latter. Frequently, local religious ceremonies, such as blessing of the fleet and prayers for success and thanksgiving, are held annually.

McEvoy (1979) gave evidence that fishery resource management was practiced by both California aboriginals, prior to European contact, and early immigrant fishermen. A California government biologist (Croker 1982) claimed that California fishermen of the 1930's to 1960's frequently requested regulations to conserve their stocks. The Alaskan Fishermen's Union in 1917 requested regulations, and that their catches be limited by "... whatever means ..." (McEvoy 1979).

During the mid 1960's while employed on a west coast salmon troller, I had numerous conversations with herring fishermen. This fishery was booming at the time. Nevertheless, one of the principal concerns of many fishermen was overexploitation and that restrictions were required. By contrast, government fishery scientists claimed that more restrictions were not required. The fishery collapsed shortly thereafter.

Discussion

The collapse of a fishery is tragic because it can be avoided with both "good science" (Cushing 1974) and, as presented in this paper, a functional system of communication with the fishermen and other industrial sectors. Were the above available at the beginning of the California sardine fishery, it may yet be extant. Instead, the sardine fishery of southern California is gone, the species being replaced by the less valuable anchovy (*Engraulis mordax* Girard). A California state legislative committee recently estimated that the sardine fishery collapse had cost the state hundreds of millions in revenue, and the fishing community thousands of jobs.

Good science (not necessarily the ultimate truth) is not easy to attain. The young field of fisheries assessment science uses ecological concepts; ecology is far from being an exact science. Consequently, it is not uncommon to have a differing of opinion amongst ecologists on the cause or consequences of certain ecological phenomena. Industry representatives used this to their advantage during their fight to stave off the setting of annual quotas for the California sardine. They employed "divide and conquer" tactics (Radovich 1981), pitting federal scientists against state biologists. Eventually, university professors were thrown into the fray.

The local scientific community requires a forum where resource assessment science can be peer reviewed. This would permit the resolution, in camera, of differences in scientific opinion and permit all to have their say. This should result in better resource science as well. A forum of this sort (CalCOFI, California Cooperative Fishery Investigations) is now active in California. If it had been in existence during the 1930's and 1940's, the fishery scientists could then have gone on the offensive rather than constantly being on the defensive, as one scientist claimed (Anonymous 1938). The conservation measures deemed appropriate could then have been presented with confidence to the industrial sectors. Evidence presented here suggests that fishermen would have listened had they been approached in a suitable manner.

In summary, this is first an appeal to scientists and fishery managers to look at government's performance regarding resource management, from the perspective of fishermen. One might then excuse the cynicism of fishermen. Secondly, that government personnel approach fishermen with the philosophy that the latter care for their resource. Thirdly, that a forum be instituted where government personnel and industrial sector delegates (fishermen tend to choose well) can meet, at least annually, to develop a management plan. My experience with advisory committees (lobster and algae) has been positive. It takes time for each to gain the confidence of the others. The scientist must present data in a format understandable to the layman; he must "come clean" and admit a lack of knowledge where appropriate. Government personnel should realize that fishermen are neither "the salt of the earth" nor fools, but people who enjoy their vocation, are knowledgeable about harvesting technology, but who tend to know little about biology or ecology. They tend to be keen to learn, but also expect an audience when prepared to talk. Croker (1982), after many years as a state of California fishery biologist, stated of fishermen "... I don't think there is any greater bunch of people to work with ..."

Acknowledgements

Thanks are extended to H. D. Johnston for realizing the need for marine plant resource management, Drs. I. Barrett and R. Lasker of the Southwest Fisheries Center for providing facilities during a sabbatical leave, and L. Prescott for technical assistance. The manuscript benefitted from reviews by Drs. M. Sinclair and R. Lasker.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on Fecundity of Chinook Salmon and its Relevance to Life History Theory

On the basis of analyses of data on fecundity and length of chinook salmon from the Sacramento and Klamath rivers (McGregor 1922, 1923) and from the Kamchatka River (Vironskiy 1972), we had recently arrived at an (unpublished) conclusion similar to that reported by Healey and Heard (1984). When contrasted with life history theory predictions, chinook "appear to delay their maturation beyond the optimum age suggested by their ocean mortality rates and changes in fecundity with age." Because Healey and Heard's analyses covered a large number of chinook stocks over a broad latitudinal range, and because more recent data used in their analyses are biased toward younger average ages of maturation than would have existed prior to heavy ocean exploitation of chinook stocks, Healey and Heard's conclusion seems well supported.

However, as Healey and Heard mentioned, total fecundity may not be an appropriate measure of age- or size-specific reproductive potential for chinook; hence, usual life history theory methods used to determine "optimum" age of maturation (Stearns 1976, 1977) may give misleading results. In particular, mean egg size may increase with increasing size of chinook salmon. Larger egg size may increase hatching success, size at emergence, and survival through emergence from gravel. Although Healey and Heard stated that there are no published data on mean egg size of chinook, McGregor (1922) did report total weights and total (estimated) egg counts for right and left ovaries from 65 aged chinook collected from the Klamath River (at Requa) from 1 August through 6 September 1921. These data may be used to estimate mean egg weights for these fish and to examine the statistical relationships between (1) mean egg size and (2) total ovary weight with fish length. McGregor reported weights in grams and lengths (probably fork lengths) in centimetres.

McGregor (1922) noted that four of his specimens had total fecundities which appeared not to follow the average trend for the majority of his specimens. Because fish were collected at the mouth of the Klamath River and the river system is large enough to support within-system (tributary-specific) variation among fecundity relations, outlier tests (Snedecor and Cochran 1967) were used to justify removal of these four data points prior to examination of relationships for total ovary weights and mean egg weights. Using linear regressions on both original and transformed (by natural logarithms, as in Healey and Heard's paper) fecundity data, the following four fish were judged outliers ($p < 0.05$): one age 4 fish with length 79 cm and total fecundity of 6468 and three age 5 fish with lengths of 92, 95, and 105 cm and total fecundities of 2013, 7946, and 8406, respectively. Based on remaining data, estimated regression equations for fecundity (F) against fish length (L) were

$$\hat{F} = -836.34 + 55.81L \quad \widehat{\ln F} = 3.077 + 1.166 \ln L.$$

Although regressions were highly significant ($F_{2,59} = 76.25$ and $F_{2,59} = 73.37$; $p < 0.001$ for both), they accounted for only about 55% of the variation in F or $\ln F$. Linear regressions of mean egg weight (W) against fish length were also highly significant for both original and transformed data ($F_{2,59} = 48.29$ and $F_{2,59} = 60.47$; $p < 0.001$ for both), but accounted for only about 50% of the variation in W or $\ln W$:

$$\hat{W} = -0.10175 + 0.00236L$$
$$\widehat{\ln W} = -14.345 + 2.696 \ln L.$$

In contrast, linear regressions of total ovary weight (O) against fish length were highly significant ($F_{2,59} = 114.87$ and $F_{2,59} = 148.66$; $p < 0.001$ for both) and accounted for 66 and 72% of the variation in O and $\ln O$:

$$\hat{O} = -823.12 + 14.36L \quad \widehat{\ln O} = -12.255 + 4.083 \ln L.$$

Total fecundity was approximately linearly related to fish length, whereas mean egg weight and total ovary weight were related approximately to the cube and fourth power of length. Total ovary weights were clearly more strongly related to fish length (or some power of fish length) than were total fecundity or mean egg weight.

Total ovary weights and mean egg weights may, of course, be confounded by state of gonad maturation. In the Klamath, Snyder (1931) found that older larger fish entered later and may have spawned within a shorter period of time after river entry than smaller younger fish. To minimize the potential confounding effect of date of river entry, data for age 3 and age 6 fish were deleted from data sets and the same analyses reported above were performed for data on age 4 and age 5 fish only; mean dates of river entry for these two groups were not significantly different (means were 23 and 22 August; $p < 0.05$). Regressions of total fecundity, total ovary weight, and mean egg weight against fish length were again all highly significant ($p < 0.001$). Incorporating age as a dummy variable in a multiple regression (Draper and Smith 1981) improved the amount of explained variation for F or $\ln F$ by only about 6%, and less so for ovary weight or mean egg weight. Tests for the significance of an age effect were ambiguous; if an age effect does exist, it is probably quite small.

The mild, approximately linear increase in total fecundity of Klamath River chinook with fish length appears related to the existence of a significant increase in mean egg weight with fish length. Because selection may be positive for both egg weight and total fecundity, variation in size-specific total fecundity and mean egg weight may be partly attributed to an absence of strong directional selection for either attribute. Egg size and total fecundity are opposing attributes in the sense that an increased number of eggs would mean a smaller mean egg size, and vice versa, for fish of a particular length. Both attributes appear constrained by a much less variable relation between total ovary weight (or volume) and fish length. The existence of a significant increasing trend of egg weight with fish length does, however, suggest that egg size may be an important survival characteristic for Klamath River chinook. We doubt that this trend is specific to the Klamath River, and we are investigating this possibility in five northern California streams.

In addition to egg size, there are several other possible advantages of large size which conventional life history theory does not address. First, it is likely that larger chinook dig deeper nests than do smaller chinook. van den Berghe and Gross (1984) reported a strong correlation between nest depth and female size for coho salmon. Deeper nests may be less prone to superimposition by smaller females and may be less susceptible to eradication due to high flows and bedload movement. Second, mating behaviors of chinook may strongly favor larger size. Preliminary observations of chinook salmon spawning behavior (supported by California Sea Grant: Hankin, unpublished) have shown that behavioral dominance on spawning grounds may be strongly size dependent. When intruding males approach a primary male (one paired with a sexually active female), outcome appears to depend on the relative sizes of males. If the intruder is smaller than the primary male it will usually be chased away, whereas if it is larger it will usually replace the primary male (see also Schroder 1981 re chum salmon). Also, female digging behaviors appear related to the sizes of approaching males. Sexually active females usually chase or bite approaching males of smaller relative sizes, whereas digging behaviors are elicited by the approach of larger males. Selection for size based on size-dependent mating success may be reflected by the fact that, for Klamath River fish at least, sizes of age 5 and 6 males actually exceeded sizes of age 5 and 6 females (Snyder 1931).

There are undoubtably many other selective advantages of large size in chinook. Ricker (1980, 1981) suggested that large size may be required for successful construction of nests in large turbulent streams with large rubble substrate. Energy requirements for long distance migrations within rivers may also favor large size and later age of maturation (see Schaffer and Elson 1975 re Atlantic salmon). Taken together, these possible selective advantages of large size in chinook salmon, and the demonstrated inheritance of age of maturation in this species (e.g. Donaldson and Menasveta 1961), make us concerned about the future viability of chinook in its natural habitats. In California, troll fishery harvests of immature chinook have significantly decreased the average age of spawners. In McGregor's and Snyder's early work on the Klamath River, spawning runs were dominated by age 4 and age 5 fish and there were good numbers of age 6 fish. Today, spawning runs are dominated by age 3 and age 4 fish, age 5 fish are rare, and age 6 fish are virtually unheard of; the 1980 run was dominated by age 2 jacks (58%; USFWS 1983). Ricker (1980, 1981) has documented similar changes throughout the chinook's range. Whether reduced numbers of smaller chinook can successfully support future intensive fisheries remains an open question. The above considerations also make us wonder just how to appropriately apply stock recruitment theory to chinook. It seems clear that neither total stock egg deposition nor total number of adults in the escapement are suitable measures of adult stock reproductive potential; it seems unlikely that the same number of (smaller) eggs carried by a (larger) spawning run of (smaller) younger fish has the same reproductive potential as the same number of (larger) eggs carried by a (smaller) spawning run of (larger) older fish.

That life history theory fails to "predict" mean age of maturation in chinook stocks appears to be a tribute to the complexity of the life history of this species. We are far from understanding why this animal's life history is so complex. But we think that Healey and Heard have made an ambitious and important contribution toward such understanding — David G. Hankin, *Department of Fisheries, Humboldt State University, Arcata, CA 95521, USA*, and Robert McKelvey, *Department of Mathematics, University of Montana, Missoula, MT 59801, USA*. (J7893a)

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Reply

We appreciate Hankin and McKelvey's supportive comments on our paper, and their presentation of additional observations which confirm the advantage of large size in chinook salmon. It is a minor point, but our comment that few data were available on chinook egg size referred to data suitable for comparing egg size and fecundity among fish of similar size. As Hankin and McKelvey point out, there appears to be a positive correlation between egg size and fish size. Rich (1925) observed this relationship for the Columbia River as well, although his data may have been biased by differing stages of maturity among large and small fish. As Hankin and McKelvey demonstrate, a number of plausible advantages to large size may be listed for chinook salmon. Furthermore, one of us (M.C.H.) has analysed age at maturity for other Pacific salmon species. The results, which will be presented elsewhere, are consistent with those for chinook in that observed age of maturity is older than that predicted by life history theory.

The apparent advantages of large size led Hankin and McKelvey to speculate that chinook populations in which the average size of spawners has declined due to selective fishing (Ricker 1981) may be unable to support intensive fisheries.

While we accept that this speculation is intuitively reasonable, the available evidence is not wholly consistent with such a gloomy prognosis. Three observations seem relevant.

The first is that chinook spawning populations typically include several age and size classes. The presence of small fish among the spawners suggests that selection cannot always favour large size. Just as it is possible to list advantages to large size, so it is possible to list advantages to small size. For example, large eggs have greater oxygen requirement than small eggs, and if buried deep in the gravel (van den Berghe and Gross 1984) are more likely to suffer from oxygen starvation at low flows than small eggs. Small adults may at times find it easier to ascend spawning tributaries than large adults, during periods of low flow for example. Younger (smaller) fish have a shorter generation time than older fish, and thus a relatively higher productivity. Presumably the age composition of any run is a compromise among the conflicting advantages to large and small size.

The second is that, although average size and age appears to have declined in many chinook populations, the age of first reproduction has not changed. The ages that now dominate spawning runs were, historically, also well represented in spawning runs. Presumably, in accordance with our comments above, these fish were successful in an evolutionary sense. Otherwise they should have been eliminated from the populations. There is no reason, in our view, to presume a low overall productivity from these age classes. In fact, having been freed from competition with larger fish for redd sites and mates, the younger age classes may be relatively more productive than formerly.

The third is that stock and recruitment data, at least for British Columbia (Healey 1982), show continually increasing recruitment throughout the period 1951–75 during which the average size of fish (Ricker 1981) and spawning stock numbers (Healey 1982) were declining rapidly. More recent recruitments have been low, but this was predicted by the stock and recruitment analysis and appears largely due to overfishing during the 1970s and early 1980s (Healey 1982), not to any fundamental change in productivity. Chinook are among the most resilient of the Pacific salmon and appear able to sustain exploitation rates in excess of 70%.

We do not mean to imply, by these observations, that managers should not be concerned about potential consequences of size selective fisheries. Rather we suggest that there is no simple way to predict what the biological consequences of such size selection will be. Even if stock productivity remains high, however, the small size of fish in the catch has important economic consequences. — M. C. Healey, *Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6,* and W. R. Heard, *U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Auke Bay Laboratory, Auke Bay, AK 99821, USA.* (J7893b)

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VAN DEN BERGHE, E. P., AND M. R. GROSS. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 41: 204–206.

BOOK REVIEWS/COMPTES RENDUS

Marine and Coastal Systems of the Quoddy Region, New Brunswick. *Martin L. H. Thomas (editor). Can. Spec. Publ. Fish. Aquat. Sci. 64. Department of Fisheries and Oceans, Ottawa, Ont. x + 306 p. 1983. $17.95.*

The northwestern New Brunswick coastline, the Quoddy region, is an area steeped in history and tradition, and blessed with scenery of unsurpassed beauty. Some of the places are familiar to us all: Passamaquoddy Bay, with its huge tides; Campobello Island, with its memories of Franklin D. Roosevelt; Grand Manaan Island, Deer Island, St. Andrews-by-the-Sea. The establishment of the St. Andrews Biological Station has ensured that the area is relatively well known to Canada's oceanographic and biological communities. The land of the Micmacs and Acadians, of spectacular golf courses, trout streams, and generations of student field trips to Huntsman Marine Biological Laboratory (HMBL), is now confronting some difficult twentieth century phenomena. Passamaquoddy Bay has long been a favoured area for tidal power development. Interest in tidal power has remained high since the 1970's oil crisis, and especially since construction of the Annapolis Royal pilot project. Point Lepreau is now the site of a nuclear generating plant, and Eastport, Maine, has been proposed as a supertanker terminus and refinery complex.

The book is therefore a timely summary of what is known about the region. It is a difficult book to classify. It is much more than a travelogue, but less than a text; more than a methods manual, yet not cutting-edge science. All the contributions were reviewed, some evidently more stringently than others. (Printing the names of referees for a volume like this is a nice professional gesture, but it effectively removes the reviewer's traditional screen of anonymity. With 24 reviewers and 17 specialized chapters, it doesn't take long to fit the two groups together.) Perhaps it is best to accept that the book is intended "as a stimulus to a better understanding of the Quoddy region" (p. 3).

The book begins with coverage of the meteorology of the region, and moves on through the various habitats (tide pools, rocky shores, etc.), then covers major animal groups (birds, fishes), and ends with coverage of the coastal forest of the area. Martin Thomas' herculean efforts are evident in that he not only contributed to the chapters on Rocky Intertidal Communities, Tide Pool Systems, and Salt Marsh Systems, but also wrote the introduction *and* the chapter on Meteorology. He is obviously a man of many talents, not the least of these being the ability to organize a book like this.

Most of the chapters include coverage of methods, and problems with the various techniques. This sort of thing is very useful, and is just what is lacking in most journals. If an author takes a couple of paragraphs to explain, in their next manuscript submitted to JFRB (pardon me, CJFAS) why a certain technique didn't work, the reviewers are virtually certain to excise that portion, leaving the next poor fellow to find out for themselves. The chapter by Wildish on Sublittoral Sedimentary Substrates is particularly good in this respect, giving grab characteristics, confidence limits for population estimates, oceanographic data, sample locations, and (great idea!) a list of suppliers of oceanographic gear, from vibracorers to plastic pails. It would also be fair to point out that the same chapter is a bit skimpy on benthic–pelagic coupling and carbon sources and sinks.

Some of the chapters stand almost by themselves as mini-treatises, or introductions to specific fields, that may be read with enjoyment by persons unfamiliar with the Quoddy region, and content to remain so. Examples are Trites and Garrett, on The Physical Oceanography of the Quoddy Region, and Gaskin, on Marine Mammals. I found the latter chapter especially interesting, and now know how to dissect a small cetacean, should I find one and wish to do so.

In a book in which the level of contributions is fairly constant, and reasonably high, the reviewer is free to choose and extoll his own favourites. I especially enjoyed Thomas, Arnold, and Taylor on Rocky Intertidal Communities, and Logan, McKay, and Noble on Sublittoral Hard Substrates. This latter chapter does an excellent job of summarizing the many years of work out of the University of New Brunswick by Logan and Noble, and integrating them with Arthur McKay's extensive survey work. The inclusion of chapters on amphibians and reptiles (Gorham and Bleakney) and coastal forests seems very apt, in a book that attempts to be Elizabethan in its coverage.

As an introduction to the Quoddy region, the book is spot-on, and timely. I do not know what the market will be — presumably every student taking HMBL courses over the next few years will want a copy, as will virtually the entire population of St. Andrews, New Brunswick. I hope, however, that the book achieves a much wider circulation than the Outer Fundy crowd, because there is much in it to interest the general student of marine science, the environmentalist, the planner, and the industrialist. Martin did a good job on the book, and the chapters he contributed to are among the book's better ones.

There are always caveats. Conspicuous by its absence is a chapter on intertidal mudflats, especially as these areas have been shown to be so important in the upper reaches of the Bay of Fundy. The editor acknowledges this lack, and pleads that a suitable contributor could not be found. One wonders whether any of several U.S. colleagues, working only an oceanographer's stone-throw away, were asked. The saltmarsh chapter is very short, though perhaps justified by the lack of extensive salt marshes in the immediate area. Reproduction of the figures is very spotty. Some of the diagrams in Steele's Coarse Sedimentary Shores chapter are virtually illegible, although some of this is due to bad choice of lettering sizes and stippling overlaps. Hinds' chapter on The Coastal Forest of the Passamaquoddy Bay Area is a welcome addition that should broaden all our horizons, but if his photographs were in focus when he handed in his manuscript he should sue someone, because *all* the figures are blurred. Typographic errors are rare throughout the book.

Perhaps it is inevitable in a compendium on a region where most research is directly government-funded, but I was struck by the vast amount of Grey Literature references — technical reports, unpublished reports, and the like. To us academics, it doesn't count if it wasn't reviewed — citing data from unpublished reports may be necessary sometimes, but to publish an idea in the same format, and then cite one's own idea as though it had survived some sort of hardnosed scrutiny, should be a no-no.

On the whole, however, the book is a first-class review of an environmentally sensitive and biologically unique region. At $17.95, it's a steal — that amounts to 6¢ per page, less than it would cost to pirate the book via a Xerox machine. If I hadn't received a review copy, I would have bought one.

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(R500)

BOOKS RECEIVED/LIVRES REÇUS

September 1984

Distribution, Biology, and Management of Exotic Fishes. *W. R. Courteney, Jr. (editor). The Johns Hopkins University Press, Baltimore, MD. 1984. xiv + 430 p. $40 cloth (U.S.). ISBN 0-8018-3037-0.* In the multi-authored book's 18 chapters, accounts of successes and failures in introductions of exotic species are presented, drawing upon the published literature and augmented by the authors' own data and experience. The book merits attention of environmentalists, wildlife managers, aquaculturists, and aquarists. [R601]

Evolution of Fish Species Flocks. *A. A. Echelle and I. Kornfield. University of Maine at Orono Press, Orono, ME (order from UMO Press, UMOP/Bookstore, University of Maine at Orono, Orono, ME 04469). 1984. x + 257 p. $20.95 paper, $28.95 cloth (U.S.). ISBN 0-89101-057-2 paper, ISBN 0-89101-058-0 cloth.* Building on work published almost 25 years ago, the multi-authored book consolidates contemporary perspectives about species flocks, including reassessments of old problems in light of current data and thought. About half of the book is devoted to non-cichlids, the other half to cichlids. [R602]

Lake Sediments and Environmental History. *E.Y. Haworth and J. W. G. Lund (editors). University of Minnesota Press, 2037 University Avenue S.E., Minneapolis, MN 55414. 1984. xviii + 411 p. $55 cloth (U.S.). ISBN 0-8166-1364-8.* The achievements of Professor Winifred Tutin in the field of paleolimnology and environmental history are honored in this book. The contributions reflect the scope of Professor Tutin's interests and contain information new to science or provide a new perspective on a particular topic. [R603]

How to Edit a Scientific Journal. *Claude T. Bishop. 1984. ISI Press, Philadelphia, PA. 1984. xii + 138 p. $14.95 in North America, $17.95 other countries (paper); $21.95 in North America, $24.95 other countries (cloth). ISBN 0-89495-034-7 paper, ISBN 0-89495-033-9 cloth.* Most scientists who accept editorial appointments are inexperienced and must teach themselves the trade. The book is concerned primarily with the review process and examines topics such as functions of editors, selection of referees, needs of an editorial office, ethics, and degree of involvement of editors in publishers' functions. [R604]

FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes. *L. J. V. Compagno. FAO Fish. Synop. 125, Vol. 4, Part 1. FAO, Rome. 1984. 249 p.* The catalogue covers all described species of living sharks and their pseudonyms, including generic and species accounts, vernacular names, keys, field marks, diagnostic characters, geographical distribution, habitat and biology, size, interest to fisheries, and literature. [R605]

The Systematics and Distributional Ecology of the Superfamily Ampeliscoida (Amphipoda: Gammaridea) in the Northeastern Pacific Region. II. The Genera *Byblis* and *Haploops*. *J. J. Dickinson. Publications in Natural Sciences 1. National Museum of Natural Sciences, Ottawa, Ont. 1984. 38 p.* Eight species of *Byblis*, five of which are new, occur on the North American continental shelf between the Bering Sea and northern California. These eight, plus five deep water species which may occur in the study area, are included in a key. *Haploops* is represented by two Arctic–boreal species; four other species likely to occur in the region are in the key. [R606]

The Amphipod Superfamily Corophioidea in the Northeastern Pacific Region. 3. Family Isaeidae: Systematics and Distributional Ecology. *K. E. Conlan. Publications in Natural Sciences 4. National Museum of Natural Sciences, Ottawa, Ont. 1983. 75 p.* The gammaridean family Isaeidae from Alaska to northern California is examined on a taxonomic, biogeographical, and ecological basis. Thirty-one species are included, of which 13 are new to science. [R607]

A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. Second Edition. *Edited by J. A. Downing and F. H. Rigler. Blackwell Scientific Publications, Inc., The Downing House, 706 Cowper Street, Palo Alto, CA. 94301. 1984. xxiv + 500 p. $55 cloth (U.S.). ISBN 0632-00616-1.* This handbook summarizes current literature and synthesizes technical progress to date. Methods for estimating zooplankton abundance, benthos of standing waters and streams, insect emergence, abundance and biomass of zooplankton, calculation and assessment of secondary productivity, respiration, statistical methods for design and analysis of samples, and study of zooplankton feeding, filtering, and assimilation are treated in this book. [R608]

Bibliographia Invertebratorum Aquaticorum Canadensium. Volume. 1. Index Generum. *D. R. Laubitz, I. Sutherland, and N. Sharma, with the assistance of Wendy Antoine. 56 p.* **Volume 2. Index Bibliographicus.** *N. Sharma, D. R. Laubitz, I. Sutherland, P. Adams, and C-t. Shih.* **Volume 3. Synopsis Speciorum.** *National Museum of Natural Sciences, Ottawa, Ont. 1983. 238 p.* The Bibliography of Canadian Invertebrates is a product of a project begun in 1973 to document as many as possible of the scientific names applied to Canadian invertebrates, to establish a list of currently recognized species, and to compile published data for each. Insects, protozoans, and ectoparasites are excluded. The indexes are available from the National Museum of Natural Sciences, Ottawa, Ont. K1A 0M8. [R609]

Survey of Invertebrate Zoologists in Canada – 1982. *C-t. Shih and D. R. Laubitz. Syllogeus 42. National Museum of Natural Sciences, Ottawa, Ont. 1983. 93 p.* Part I lists invertebrate zoologists, taxonomic groups studied, and geographic and ecological areas dealt with. Part II is a taxonomic cross-reference to Part I. [R610]

A Checklist and Bibliography of the Sipuncula from Canadian and Adjacent Waters. *P. G. Frank. Syllogeus 46. National Museum of Natural Sciences, Ottawa, Ont. 1983. 47 p.* Seventeen species of Sipuncula are briefly described, with synonymies, detailed distribution, and sources of the information included. [R611]

Climatic Change in Canada 3. *Edited by C. R. Harrington. Syllogeus 49. National Museum of Natural Sciences, Ottawa, Ont. 1983. 343 p.* The third publication in a series arising from the National Museum of Natural Sciences' climatic change project, this multi-authored volume presents results of studies of various subjects which can provide evidence of climatic changes, e.g. sea ice conditions, tree rings, ice cores, and vegetation patterns. Two papers on future climate in Canada are also included. [R613]

Special Issue on Historical Whaling Records. *Edited by M. F. Tillman and G. P. Donovan. Reports of the International Whaling Commission Special Issue No. 5. International Whaling Commission, Cambridge. 1983. 269 p. $35 U.S. ISBN 0-906975-11-5.* This volume contains the report of activities of the International Workshop on Historical Whaling Records in September 1977. Seven additional papers presented to the Scientific Committee between 1980 and 1982 are included, as they further demonstrate the value of studying historical records. [R615]

Reproduction in Whales, Dolphins and Porpoises. *Edited by W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster. Reports of the International Whaling Commission. Special Issue No. 6. International Whaling Commission, Cambridge. 1983. 495 p. $40 U.S. ISBN 0-906975-07-7.* The volume comprises the proceedings of the conference, Cetacean Reproduction: Estimating Parameters for Stock Assessment and Management, held in La Jolla in 1981. The sessions dealt with reviews of cetacean reproduction, problems and new approaches in methodology, population case studies, density-dependence, and behavior, functional morphology, and physiology. [R616]

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTS PUBLICATIONS

VOLUME 41, No. 10 — article by J. C. Priscu and L. R. Priscu: *Inorganic nitrogen uptake in oligotrophic Lake Taupo, New Zealand.*

Page 1439, caption to Table 1: the last phrase should read "italicized values are from NH_4^+ uptake kinetics experiments …"

VOLUME 41, No. 10 — note by D. J. Carlson, D. W. Townsend, A. L. Hilyard, and J. F. Eaton: *Effect of an intertidal mudflat on plankton of the overlying water column.*

Page 1528: The following reference was inadvertently omitted from the reference list: Mayer, L. M., P. T. Rachain, W. Guerin, S. A. Macko, L. Watling, and F. E. Anderson. 1984. Biological and granulometric controls on sedimentary organic matter of an intertidal mudflat. Estuarine Coastal Shelf Sci. (In press)

VOLUME 41, No. 11 — article by B. D. LaZerte and P. J. Dillon: *Relative importance of anthropogenic versus natural sources of acidity in lakes and streams of central Ontario.*

Page 1675, left column: formula (1) should read as follows:

$$(1) \quad -\log_{10}(K_h) = 0.96 + 0.90 \cdot \mathrm{pH} - 0.039 \cdot \mathrm{pH}^2$$

VOLUME 41, No. 12 — article by G. L. Carper and R. W. Bachmann: *Wind resuspension of sediments in a prairie lake.*

Page 1764, left column, 3rd line from bottom: sentence should read "Sampling occurred on 41 days."

VOLUME 41, No. 12 — article by R. M. Peterman and F. Y. C. Wong: *Cross correlations between reconstructed ocean abundances of Bristol Bay and British Columbia sockeye salmon (Oncorhynchus nerka).*

Page 1816, left column, 1st line: "311" should read "211".

ANNOUNCEMENTS/AVIS

CALL FOR PAPERS

7–10 October, 1985

Workshop on the Statistical Aspects of Water Quality Monitoring to be held at the Canada Centre for Inland Waters, Burlington, Ont., Canada

Scientists, statisticians, and users of statistical methods in limnology, regulation and water quality control, monitoring network design and modelling of aquatic environments, are invited to participate in this Workshop. Information can be obtained from A. El-Shaarawi, Aquatic Physics and Systems Division, NWRI, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ont. L7R 4A6, telephone (416) 637-4534, or R. E. Kwiatkowski, Water Quality Branch, IWD, Place Vincent Massey, Ottawa, Ont. K1A 0E7, telephone (819) 997-1921.

DEMANDE D'EXPOSÉS

7–10 octobre 1985

Atelier sur les aspects statistiques du contrôle de la qualité de l'eau, au Centre canadien des eaux intérieures, Burlington (Ont.), Canada

Les scientifiques, statisticiens et utilisateurs des méthodes statistiques en limnologie, réglementation et contrôle de la qualité de l'eau, conception de réseaux de surveillance et modélisation des milieux aquatiques, sont invités à participer à cet atelier. Pour plus de renseignements, s'adresser à A. El-Shaarawi, Division de la physique aquatique et des systèmes, INRE, Centre canadien des eaux intérieures, C.P. 5050, Burlington (Ont.) L7R 4A6, téléphone (416) 637-4534, ou à R. E. Kwiatkowski, Direction de la qualité des eaux, DGEI, Place Vincent Massey, Ottawa (Ont.) K1A 0E7, téléphone (819) 997-1921.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Identifying pollution related changes in chironomid communities as a function of taxonomic rank **J. C. Waterhouse and M. P. Farrell**

A general theory for analysis of catch and effort data **J. Schnute**

How do bottlenose dolphins, *Tursiops truncatus*, react to oil films under different light conditions? **D. J. St. Aubin, J. R. Geraci, T. G. Smith, and T. G. Friesen**

Biochemical genetic stock identification of chum salmon (*Oncorhynchus keta*) in southern British Columbia **T. D. Beacham, R. E. Withler, and A. P. Gould**

Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s **E. W. Eck and E. H. Brown, Jr.**

Discrimination d'un stock de poisson, l'anguille (*Anguilla rostrata*), basée sur la présence d'un produit chimique de synthèse, le mirex **J.-D. Dutil, B. Légaré et C. Desjardins**

Estimating the population dynamics of coho salmon (*Oncorhynchus kisutch*) using pooled time-series and cross-sectional data **J. L. Anderson and J. E. Wilen**

Estimation of harp seal (*Phoca groenlandica*) pup production from age samples **J. G. Cooke**

Morphological, electrophoretic, and fecundity characteristics of Atlantic snow crab (*Chionoecetes opilio*), and implications for fisheries management **K. Davidson, J. C. Roff, and R. W. Elner**

Diet and digestion rates of slimy sculpin, *Cottus cognatus*, in an Alaskan arctic lake **A. E. Hershey and M. E. McDonald**

Behavior of rainbow trout (*Salmo gairdneri*) and white perch (*Morone americana*): effects of attaching telemetry transmitters **E. J. Mellas and J. M. Haynes**

Introduction to limnological research at Saqvaqjuac, northern Hudson Bay **H. E. Welch**

Water circulation in small arctic lakes in winter **H. E. Welch and M. A. Bergmann**

Winter respiration of lakes at Saqvaqjuac, N.W.T. **H. E. Welch and M. A. Bergmann**

Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) **S. D. McCormick, R. J. Naiman, and E. T. Montgomery**

Patterns of growth and smolting of Atlantic salmon (*Salmo salar*) parr in a southwestern Newfoundland river **G. T. Evans, J. C. Rice, and E. M. P. Chadwick**

Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, 1970–79 **E. M. Levy**

Rates of food exploitation by littoral fishes in a mesotrophic north-temperate lake **D. Boisclair and W. C. Leggett**

Factors regulating in situ filtering rates of Cladocera **P. Chow-Fraser and R. Knoechel**

Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence **D. M. Ware and T. C. Lambert**

Notes

Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts **B. Jonsson and J. Ruud-Hansen**

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A manual of chemical and biological methods for seawater analysis (edited by T. R. Parsons, Y. Maita, and C. Lalli) **J. R. Forbes**

A manual on methods for the assessment of secondary productivity in fresh waters (edited by John A. Downing and Frank H. Rigler) **J. C. Roff**

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Northern Science Award

The International Polar Year, 1882–83, was the first worldwide coordinated scientific enterprise and the most significant single event in the founding of the science of geophysics. The Centenary Medal was created to mark the 100th Anniversary of the International Polar Year, 1882–83, and to give recognition of Canada's part in it. The medal together with a prize of $5000 will, henceforth, be awarded annually to an individual who has made distinguished contributions to Northern Canada through scientific activity. A 5-member selection committee appointed by the Minister of Indian Affairs and Northern Development recommends the recipient. Anyone may make a nomination. The nominator should provide a letter of nomination setting out clearly the case in favour of the candidate. Inquiries and nominations should be sent to:

Northern Research and Science Advisor, Indian and Northern Affairs Canada, Ottawa, Ont. K1A 0H4.

Prix de la recherche scientifique sur le nord

L'Année polaire internationale, en 1882–83, a été la première entreprise scientifique internationale concertée et l'événement le plus important dans l'élaboration d'une science authentique de la géophysique. Le Prix de la recherche scientifique sur le Nord a été créé pour marquer le 100^{e} anniversaire de l'Année internationale et pour y souligner la participation du Canada. En vertu du Prix, la Médaille du centenaire de l'API, accompagnée d'une somme de 5000 $, sera décernée chaque année à une personne qui, dans son domaine de compétence scientifique, a contribué de façon remarquable à l'avancement des connaissances sur le Nord canadien. Un jury de 5 membres établi par le ministre des Affaires indiennes et du Nord canadien, recommande le récipiendaire. Toute personne intéressée peut proposer un candidat. L'auteur de la proposition doit envoyer une lettre de présentation énonçant clairement les raisons pour lesquelles il propose la candidature. Les demandes de renseignements et les propositions de candidature doivent être adressées au :

Conseiller scientifique sur le Nord, Affaires indiennes et du Nord Canada, Ottawa (Ont.) K1A 0H4.

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